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CONTENTS

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THE MYRMECOPHILOUS PTINIDAE (COLEOPTERA), WITH A KEY TO AUSTRALIAN SPECIES

JOHN F. LAWRENCE[1] AND HANS REICHARDT[2]

CONTENTS

ABSTRACT

A review is presented of the current knowledge on ptinid beetles known to occur with ants. Included are: 1) a catalogue of the myrmecophilous Ptinidae, 2) a summary of biological and distributional data, 3) a revision of the genera and key to the species occurring in Australia, and 4) a discussion of the origin and evolution of myrmecophily in the family. Eight genera and 43 species are treated, and 8 previously recognized genera are placed into synonymy. A list of ant host species is also given.

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INTRODUCTION

The family Ptinidae includes about 50 genera and 600 species, which are distributed throughout the major regions of the world but are particularly abundant in the drier parts of the subtropical and temperate zones. Of the described species, almost 50 have been recorded from the nests of ants and at least 42 appear to be true inquilines. The purposes of this paper are (1) to propose certain changes in the classification of the myrmecophilous species on the basis of newly discovered characters, (2) to provide a key to the species occurring in Australia, (3) to summarize what is presently known about the biology and distribution of myrmecophilous ptinids in the form of a catalogue, and (4) to speculate on the possible origin and evolution of myrmecophily in the family.

Those species of Ptinidae which are here considered to be true ant guests fall into five main groups: the two tropical American genera *Gnostus* and *Fabrasia*, the South African *Diplocotidus*, the southeast Asian genus *Myrmecoptinus*, and the several Australian genera which have usually been placed in the subfamily Ectrephinae. The first four of these will be discussed briefly below and the last will be treated in detail in a later section.

In addition to the above, several ptinids have been recorded from the nests of ants. The European *Ptinus subpilosus* Sturm and *P. sexpunctatus* Panzer have been taken with the ants *Acanthomyops fuliginosus*

(Latreille) and *A. brunneus* (Latreille); both beetles occur in other habitats as well (Linsley, 1944; Howe, 1959). The species *Diplocotidus moseri* Brauns was described from specimens collected under a rock with the ant *Meranoplus peringueyi* Emery in South Africa (Wasmann and Brauns, 1925). Andreae (*in litt.*) has examined the type and considers it to be an old and rubbed specimen of *Pseudomezium coquereli* (Fairmaire). This record with ants is probably accidental. Finally, the species *Leioptinus inflatus* Wasmann (1928) was described from a nest of *Myrmicaria arachnoides* Smith on Sumatra. This species may be myrmecophilous, but from the description and illustration it does not appear to us to belong in the family Ptinidae.

Gnostus and *Fabrasia*.—These two genera, which contain all of the New World myrmecophiles, have been treated elsewhere (Lawrence and Reichardt, 1966a) and will not be discussed in detail here. Since the publication of the above revision, however, two new records have come to our attention. A specimen of *Fabrasia borgmeieri* Lawrence and Reichardt, in the collection of the Departamento de Zoologia, was collected at Poços de Caldas, Minas Gerais, Brazil, in February, 1933, with the ant *Camponotus* (*Myrmobrachys*) *senex* (F. Smith). This represents a southern range extension and a new species of ant host. A specimen of *F. wheeleri* Lawrence and Reichardt, in the collection of the California Insect Survey, was collected 6.3 miles west of Tehuantepec, Oaxaca, Mexico, on July 21, 1952, by E. E. Gilbert and C. D. MacNeill (ant host not recorded). This is the first record of *Fabrasia* from Mexico and represents a considerable northern range extension for *F. wheeleri*, known previously from Colombia.

Diplocotidus.—With the removal of *D. moseri* (see above), this genus contains a single species, *D. formicola* Peringuey, which occurs in the interior of South Africa. Andreae (*in litt.*) considers these to be true myrmecophiles and has seen two undescribed species from the same area. The species differs considerably from other myrmecophilous ptinids and probably represents an independent line. The construction of the prothorax (Fig. 29), the subquadrate and concave clypeus (Fig. 3), and the aedeagus with reduced parameres (Figs. 26, 27) are all unique. The grooves on the pronotum are somewhat similar to those of *P. coquereli* and some of the South African gibbiines, but the species does not appear to be closely related to any of these.

Myrmecoptinus.—*Myrmecoptinus butteli* Wasmann (1916) was described from Sumatra and associated with the ant *Crematogaster butteli* Forel. Although Wasmann's type has not been examined, several specimens have been seen from Ceylon, Borneo, China, North Vietnam, and Burma that conform fairly well with the description and probably belong in the same group. The elytral humeri are well developed, the wings are present, the clypeus is flattened and triangular like that in *Ptinus* (Fig. 2), and antennal modifications are completely absent. The pronotum is relatively simple but has a well-defined, narrow, transverse groove at the base, which connects lateral pairs of processes resembling the trichomes found in other inquilines. The color is black and the vestiture is sparse, consisting of fine hairs as in other myrmecophilous forms. One of the specimens examined was collected by Mjöberg in an ant nest, but the locality is indecipherable. These beetles are probably myrmecophiles, but they do not appear to be closely related to the other groups.

Ectrephinae.—The majority of myrmecophilous Ptinidae occur in Australia and are generally placed in the subfamily Ectrephinae. These will be discussed further below.

Notes on Terminology

There are a few terms used in the key and discussions that may need clarification, although the usage is essentially the same

as that found in Lawrence and Reichardt (1966a).

Clypeus. This is equivalent to the area referred to by Stickney (1923) as the post-clypeus. In most Ptinidae it consists of a well-defined, broad, triangular plate lying just in front of and between the antennal fossae, the anatomical base of the plate forming the apex of the triangle (Fig. 2). The word "apex" in the text refers to the anatomical apex to which the labrum is attached. Many of the myrmecophilous species have a more elongate and tumid clypeus (Figs. 1, 4, 7, 8), while in several others it consists of a flattened, cleft plate (Figs. 5, 6, 9, 10).

Trichomes. In the supplement to Torre-Bueno's *Glossary of Entomology* (Tulloch, 1960), trichomes are defined as "modified hairs present on certain myrmecophilous insects which give off secretions which ants imbibe." Although the word may be used to describe any group of hairs which are thought to be glandular, it is commonly restricted to distinct setiferous processes usually found on the prothorax, antennae, elytra, or abdomen of myrmecophilous beetles. Actually, statements about the function of these structures are seldom, if ever, accompanied by histological or behavioral studies (see p. 12).

In the Ptinidae there are four main kinds of structures which may be glandular: (1) elytral pores, (2) femoral trichomes, (3) pronotal trichomes, and (4) antennal pilosity. The first two structures are found only in the genus *Fabrasia*; the elytral pores secrete a white waxlike substance. In some ptinids, such as *Ectrephes formicarum* Pascoe (Fig. 28) and *Enasiba tristis* Olliff, the pronotal trichomes bear distinct pubescence and resemble those occurring in the Paussidae (Darlington, 1950). Many species, however, have lateral clefts and processes (Figs. 30–32, 34) that appear to be homologous to the trichomes of *E. formicarum* but that do not bear patches of hairs. One feature that all of these structures share is the proximity of the tips of two processes arising on different sides of a cleft or fovea. Perhaps this is a device for collecting a drop of liquid. In the following discussions all of these prothoracic structures are called trichomes. Patches of short hairs or pile are usually found on the last antennal segment (Figs. 17–19), and in some species they are concealed within a concavity at the tip of the segment (Figs. 15, 16). Occasionally the hairs may be absent (or rubbed off), but the extremely fine punctation may indicate the presence of a glandular area (Fig. 22).

Measurements. The total length is the maximum length as measured from above (tips of elytra to the most anterior point of the clypeus). EL and EW refer to greatest elytral length and greatest elytral width, respectively.

CLASSIFICATION OF MYRMECOPHILES

The placement of myrmecophiles in a system of classification has always presented a problem to taxonomists because of the development in these forms of special adaptations associated with inquilinous habits. In some groups normally conservative characters, such as the number or shape of antennal segments, may be highly variable, while in others entirely new structures, such as trichomes, may be present. It is not surprising that a number of these species have been placed in separate families until more careful studies have clarified their relationships. A few of the many beetle families originally proposed for the inclusion of inquilines but no longer recognized are the Pseudomorphidae (Carabidae), Clavigeridae (Pselaphidae), Rhysopaussidae (Tenebrionidae), and Cossyphodidae (Tenebrionidae).

During the last hundred years there has been considerable difference of opinion as to the placement of the myrmecophilous ptinids within the higher classification of the Coleoptera. Although Westwood (1855) considered *Gnostus* to be related to the Xylophaga of Latreille, later workers placed it near the Paussidae, Pselaphidae,

or Scydmaenidae; the taxonomic history of the genus is discussed by Lawrence and Reichardt (1966a). Pascoe (1866) compared his genus *Ectrephes* with *Gnostus* and the Paussidae. Gemminger and Harold (1869) proposed the family Gnostidae to include both *Gnostus* and *Ectrephes*, while Wasmann (1894) proposed the family Ectrephidae for *Ectrephes* and Westwood's two genera *Diplocotes* and *Polyplocotes*. Sharp and Muir (1912) noted the similarities between *Polyplocotes* and *Ptinus* with respect to the basal connection of the lateral and median lobes of the aedeagus. In 1916, both Wasmann and Mjöberg treated the ectrephines as members of the Ptinidae. Forbes (1926) pointed out the relationship of *Gnostus* to the ptinids on the basis of wing venation, but the complete absence of wings in the ectrephines made a similar comparison impossible. Our studies definitely confirm the inclusion of this group within the Ptinidae. *Diplocotes familiaris* (Olliff), one of the least specialized of the Australian species, differs little from other wingless ptinids, and a gradation can be seen from *D. familiaris* to the highly modified forms discussed below. The aedeagi of *D. familiaris* (Fig. 23), *D. laticornis* (Lea) (Fig. 24), and *Ectrephes formicarum* Pascoe (Fig. 25) all have the same basic structure found in *Gnostus* and *Fabrasia* (Lawrence and Reichardt, 1966a) and in various other ptinids (Hinton, 1941).

Within the Ptinidae, the classification of these myrmecophilous species presents a problem, owing to the present need for a complete revision of the family. Two subgroups, the Gibbiinae and the Ptininae, are usually recognized. In the former, the elytra are laterally compressed and partly enclose the reduced abdomen; the group includes *Gibbium*, *Mezium*, *Damarus*, and a few other genera, the species of which are most abundant in South Africa. The remainder of the ptinids are usually included in the Ptininae, which contains a diverse assemblage of forms.

The inclusion of various myrmecophilous species in the family has led to the proposal of several more subfamilies. The genus *Ectrephes* Pascoe, along with Westwood's genera *Diplocotes* and *Polyplocotes* and Olliff's *Enasiba* and *Diphobia*, was placed in the Ectrephinae, while *Gnostus* was placed in the Gnostinae. Mjöberg (1916) divided the ectrephines into three subfamilies: Polyplocotinae, containing most of the species; Paussoptininae, for those species with flattened antennal segments; and Ectrephinae, including those species originally placed in *Ectrephes*. He placed *Diphobia* and the South African genus *Diplocotidus* Peringuey in the subfamily Ptininae, because of the lack of antennal modifications. Martinez and Viana (1965) proposed the name Fabrasiinae for the genus *Fabrasia*, and Costa Lima (1962) placed his genus *Plaumanniola* in the Plaumanniolinae. The latter genus was found to belong to the family Scydmaenidae (Lawrence and Reichardt, 1966b).

We are of the opinion that there are at least five independent stocks of myrmecophilous ptinids: *Gnostus*, *Fabrasia*, *Diplocotidus*, *Myrmecoptinus*, and the ectrephines. The last group may be divided into two subgroups (see below), but their derivation from a single ancestor is indicated by the numerous parallelisms displayed by the two. *Myrmecoptinus* differs only slightly from the ptinines and could hardly be placed in a separate subfamily. *Gnostus* and *Fabrasia*, on the other hand, are quite distinct, although they are derivable from some of the more elongate and parallel-sided winged Ptininae. *Diplocotidus* is also a very distinct form and might well be placed in a separate subfamily, for which a new name would be required. The Ectrephinae are linked with the Ptininae by forms like *D. familiaris*, and the only character which could be used to distinguish the two groups is the form of the clypeus, which is elongate and tumid or cleft in *Diplocotes* and its relatives. If subfamilies or tribes are recognized, then, four would be required: one for each of the

Neotropical groups, one for the South African *Diplocotidus*, and one for the Australian ectrephines.

The second problem is whether or not these myrmecophilous forms are different enough from other ptinids to be placed in separate groups and what rank to assign to these groups. Within the large subfamily Ptininae, there are several other clusters of genera which are just as distinct, or more so, if one disregards the special adaptations of myrmecophiles. These include: *Diegous* and *Xylodes* from Mauritius; *Casopus* and its relatives from the Canary Islands; *Cylindroptinus* and its relatives from Southeast Asia; *Niptus* and its allies; *Sphaericus*; and *Trigonogenius*. Until a thorough study is made of the generic classification in the family Ptinidae, we think it serves no useful purpose to place the inquilinous species in separate subfamilies or tribes.

THE AUSTRALIAN ECTREPHINES

The 35 described species of myrmecophilous ptinids inhabiting Australia are generally placed within 14 genera, which are characterized mainly on the basis of antennal segmentation. *Diphobia* Olliff contains species with relatively simple, 11-segmented antennae (Fig. 21). Those species in which the penultimate antennal segment is enlarged (Figs. 17, 18) are placed in three genera according to the total number of antennal segments: *Diplocotes* Westwood (11), *Decemplocotes* Mjöberg (10), and *Polyplocotes* Westwood (9). In the monotypic *Hexaplocotes* Lea, the antennae are 6-segmented and the last two segments are enlarged and flattened (Fig. 22). In several species the antennal segments are strongly compressed and may be partially or completely fused to form a club (Figs. 19, 20); these forms have been placed in *Paussoptinus* Lea (10 segments; see p. 9), *Leaptinus* Mjöberg (10 segments), *Paussoceros* Mjöberg (9 segments), *Pseudectrephes* Pic (7 segments), *Monectrephes* Mjöberg (3 segments; see p. 10), and *Mesectrephes* Mjöberg (3 segments). In *Ectrephes* Pascoe the antennae are 3-segmented and the last segment forms a solid, cylindrical club (Fig. 15), while in *Bitrephes* Oke they are 2-segmented and the terminal segment is somewhat wedge-shaped (Fig. 35). Finally, in the genus *Enasiba* Olliff the antennal segments are peculiarly shaped, as in Figure 16, and the pronotum is elongate, with four trichomes.

We feel that the above classification is unnatural for several reasons. First, any classification which relies so heavily on a single character complex is suspect. Furthermore, the particular characters used are highly variable within the group and are associated with a narrow specialization; thus they would have a low taxonomic weight according to the tenets originally proposed by Darwin. The adaptive nature of the antennal modifications becomes obvious if one considers the numerous cases of convergence with respect to these characters in unrelated myrmecophilous groups. The short, stump-like antenna of *Ectrephes formicarum* (Fig. 15), for instance, is very similar to that of *Gnostus*, and the same type of antenna may be found in several unrelated myrmecophiles, such as *Euclarkia* (Colydiidae), *Trochoideus* (Endomychidae), *Fustiger* (Pselaphidae), and *Paussus* (Paussidae). Another objection is the lack of correlation of antennal characters with other features; *Diplocotes armicollis*, *Paussoptinus laticornis*, and *Mesectrephes kingi*, for instance, have very different antennal types and yet are similar with respect to the pronotum and clypeus. A further criticism may be made of the use of meristic characters (number of antennal segments), which should be given low weight for obvious reasons. The independent loss or fusion of antennal segments has been demonstrated in a number of beetle groups (Chapin, 1965, for the Coccinellidae; Lawrence, 1967, for the Ciidae), and extreme parallel reductions in myrmecophilous beetles have been discussed by Darlington (1950) for the Paussidae and Park (1942) for the Pselaphidae.

In an attempt to find other characters to use in classifying these Australian species, a study was made of the clypeal region. This structure had been ignored in the past because most of the specimens were glued to cards. In most Ptinidae the clypeus is broadly triangular and somewhat flattened, and the labrum is small and transverse (Fig. 2). With the exception of *Myrmecoptinus butteli*, all of the myrmecophilous species have the clypeus somewhat modified. The Australian forms fall into two distinct groups on the basis of clypeal structure. In the first group (Figs. 1, 4, 7, 8), the clypeus is slightly to strongly tumid and subtriangular, with the median portion, at least, distinctly punctate. In the second group (Figs. 5, 6, 9, 10), the clypeus is elevated, flattened, and deeply cleft at the apex, forming a U-shaped clypeal plate, which is impunctate and shiny. The species included in each group are given below according to their present generic assignments:

Group I: *Diphobia familiaris, D. foveata, D. intricata, D. longicornis, D. metallica, D. myrmecophila, Diplocotes armicollis, D. foveicollis, D. howittanus, D. minuta, Decemplocotes brevipennis,* D. strigicollis, Polyplocotes apicalis, P. carinaticeps, P. pilosus,* P. similis, Paussoptinus laticornis, Mesectrephes kingi*, and *Bitrephes cuneiformis.*

Group II: *Polyplocotes castaneus, P. longicollis, P. longipes, P. nitidus, P. ovipennis, P. perforatus, P. scabricollis,* Hexaplocotes sulcifrons, Leaptinus dolichognathus, Paussoceros antennalis,* P. cremastogastri, Pseudectrephes clavatus,* Monectrephes pascoei, Ectrephes formicarum, Enasiba tristis*, and *E. microcera.*

The types of those species marked with an asterisk have not been examined, but in every case the descriptions, illustrations, or comparisons with known species have been sufficient to place the species with a reasonable degree of certainty in one group or the other.

Since the first type of clypeus is the most easily derivable from that occurring in most Ptinidae and since the simplest type of antenna also occurs in the first group, it is reasonable to assume that this clypeal type is primitive. The joint possession of a relatively complex and derived clypeus by members of group II and the occurrence within each group of characteristic antennal and pronotal types present strong evidence that the division is a natural one. The parallel development of certain antennal modifications in the two groups is not surprising for myrmecophiles and would tend to support the ultimate derivation of both stocks from a common ancestor.

Within group I, it is difficult to segregate the species further without using too many generic names. If the antennae are used, five genera might be recognized, when meristic differences are ignored in the group characterized by having an enlarged penultimate antennal segment. In the structure of the prothorax, *D. armicollis, P. laticornis, P. carinaticeps, M. kingi*, and *B. cuneiformis* are similar (Figs. 30 and 35), but *D. foveicollis* is intermediate in this respect between these species and the remainder of group I. The clypeus of *P. carinaticeps* (Fig. 7) is unique in that it forms a narrow, median ridge, but that of *M. kingi* (Fig. 8) might well represent an intermediate condition. We think the most practical solution would be to consider all of the species in group I as belonging to a single genus, the oldest name for which is *Diplocotes* Westwood.

Within group II, there are at least three distinct subgroups. The genus *Enasiba* is readily distinguishable on the basis of pronotal and antennal structure (Fig. 16). *Ectrephes formicarum, Monectrephes pascoei*, and *Pseudectrephes clavatus* may be united on the basis of pronotal structure; the pronotum has sharp lateral edges and the trichomes are lateral and similar in form (Fig. 28). *Ectrephes* is the oldest name for this genus. The remaining species do not vary considerably with respect to pronotal and antennal characters and are all in-

cluded in the genus *Polyplocotes* Westwood.

Although the generic classification presented here represents an improvement over the older classification, further modification may still be needed. When more species or character complexes are studied, it may be necessary to further subdivide the genera. A key to the genera and species of ectrephines is included below, followed by a brief discussion of each genus as it is here delimited. A résumé of the proposed classification, with generic and specific synonymies, is given in a later section.

Key to the Genera and Species of Myrmecophilous Ptinidae Occurring in Australia

1. Clypeus usually subtriangular (Figs. 1, 4), slightly to strongly tumid, occasionally elevated, forming a narrow, median ridge (Figs. 7, 8) (genus *Diplocotes* Westwood) 2
— Clypeus elevated, flattened, and deeply cleft at apex, forming a U-shaped clypeal plate (Figs. 5, 6, 9, 10) 20
2. Antennae 11-segmented 3
— Antennae with less than 11 segments 12
3. Antennal segment 10 not enlarged, shorter than segment 11 (Fig. 21) 4
— Antennal segment 10 enlarged, longer than segment 11 and usually as long as segments 8 and 9 combined (Fig. 17) 9
4. Antennal segment 11 very long, as long as segments 8 to 10 combined .... *D. longicornis* (Lea)
— Antennal segment 11 not as long as segments 8 to 10 combined 5
5. Pronotum without basolateral trichomes, occasionally with weak lateral foveae 6
— Pronotum with distinct basolateral trichomes and deep lateral foveae 7
6. Elytra shorter and broader, EL/EW less than 1.25, dark metallic blue in color, the punctation not distinctly seriate, each puncture rounded and bearing a relatively long, suberect hair .... *D. metallicus* (Lea)
— Elytra longer and narrower, EL/EW more than 1.25, reddish brown in color, the punctation distinctly seriate, each puncture elongate and bearing a very short, decumbent hair .... *D. myrmecophilus* (Lea)
7. Antennal segments 6–10 shorter than broad, compressed, each segment bearing at the apex 4 brushes of yellow hairs .... *D. intricatus* (Lea)
— Antennal segments 6–10 as long as or longer than broad, not compressed, and without brushes of yellow hairs 8
8. Elytral punctures very small and shallow, scarcely visible under lower magnification; pronotum without basomesal fovea .... *D. familiaris* (Olliff)
— Elytral punctures larger and more deeply impressed; pronotum with basomesal fovea .... *D. foveatus* (Lea)
9. Pronotum expanded apically forming 2 lateral projections 10
— Pronotum without apicolateral projections 11
10. Pronotum about as long as wide at base, apicolateral projection consisting of a sharp tooth; elytral punctures bearing very short, decumbent hairs .... *D. armicollis* Lea
— Pronotum more than 1.25 × as long as wide at base, apicolateral projection consisting of a rounded process bearing several small tubercles; elytral punctures bearing relatively long, suberect hairs .... *D. foveicollis* Olliff
11. Total length more than 1.50 mm; basal impression of pronotum not expanded in middle .... *D. howittanus* Westwood
— Total length less than 1.25 mm; basal impression of pronotum slightly expanded in middle forming a shallow fovea .... *D. minutus* Oke
12. Antennae 10-segmented 13
— Antennae with less than 10 segments 15
13. Antennal segments 2–10 strongly compressed (Fig. 19) .... *D. laticornis* (Lea)
— Antennal segments 2–10 not compressed 14
14. Pronotum with basolateral trichomes .... *D. brevipennis* (Pic)
— Pronotum without basolateral trichomes .... *D. strigicollis* Lea
15. Antennae 9-segmented 16
— Antennae with less than 9 segments 19
16. Clypeus elevated in middle, forming a narrow ridge (Fig. 7); pronotum shorter than wide at base, with apicolateral teeth .... *D. carinaticeps* (Oke)
— Clypeus somewhat tumid, but not forming a narrow ridge (Fig. 8); pronotum more than 1.20 × as long as wide at base, without apicolateral teeth 17
17. Antennal segment 9 longer than 8 .... *D. apicalis* (Oke)
— Antennal segment 8 longer than 9 18
18. Total length less than 2.50 mm; elytral punctures bearing very short, decumbent hairs .... *D. similis* (Oke)
— Total length more than 2.50 mm; elytral punctures bearing relatively long, suberect hairs .... *D. pilosus* (Mjöberg)

19. Antennae with 3 segments, the last segment strongly compressed .... *D. kingi* (Westwood)
— Antennae with 2 segments, the last segment wedge-shaped (Fig. 35) .... *D. cuneiformis* (Oke)
20. Pronotum with a narrow, median, longitudinal groove, and with 2 lateral and 2 mesal trichomes within a transverse basal impression; antennal segments 2 and 3 broadly joined, segments 3–5 somewhat triangular or wedge-shaped with the base broader than the apex, and segments 6–10 somewhat compressed (Fig. 16) (genus *Enasiba* Olliff) 21
— Pronotum without a median, longitudinal groove, without trichomes or with only 2 lateral ones 22
21. Head, pronotum, and bases of elytra bearing short, stout bristles, which are less than 3 × as long as wide; remainder of elytra bearing very short and fine hairs, which are barely visible under lower magnification; antennal segments 3–5 only slightly broader at base than at apex .... *E. microcera* Clark
— Head, pronotum, and elytra bearing longer and finer bristles, which are about 8 × as long as wide; antennal segments 3–5 much broader at base than at apex .... *E. tristis* Olliff
22. Pronotum without lateral margins (Figs. 33, 34) (genus *Polyplocotes* Westwood) 23
— Pronotum with sharp lateral margins (Fig. 28) (genus *Ectrephes* Pascoe) 33
23. Antennae 10-segmented, segments 3–10 compressed .... *P. dolichognathus* (Lea)
— Antennae with less than 10 segments 24
24. Antennae 6-segmented, with the last 2 segments enlarged and compressed (Fig. 22) .... *P. sulcifrons* (Lea)
— Antennae 9-segmented 25
25. Antennal segments 3–9 compressed 26
— Antennal segments 8 and 9 or none of them compressed 27
26. Total length more than 2.50 mm; 9th antennal segment buried within the apex of the 8th .... *P. antennalis* (Mjöberg)
— Total length less than 2.50 mm; 9th antennal segment not buried within the apex of 8th .... *P. cremastogastri* (Lea)
27. Pronotum without basolateral trichomes or a basal impression; mesal portion of pronotal disc strigose (Fig. 33); clypeal plate with a lateral perforation beneath it .... *P. perforatus* Lea
— Pronotum with basolateral trichomes; if basal impression absent, then mesal portion of pronotal disc not strigose; clypeus without perforation 28
28. Pronotum without basal impression; mesal portion of pronotal disc not longitudinally strigose .... *P. nitidus* Westwood
— Pronotum with basal impression; mesal portion of pronotal disc longitudinally strigose, at least basally (Fig. 34) 29
29. Antennal segment 3 almost 3 × as long as wide .... *P. longipes* Lea
— Antennal segment 3 not more than 1.50 × as long as wide 30
30. Highest portion of pronotal disc very finely and sparsely punctate and shiny; anterior edge of pronotum with a transverse row of deep punctures (Fig. 34) .... *P. longicollis* Westwood
— Highest portion of pronotal disc more coarsely and densely punctate, granulate, or strigose, not shiny; anterior edge of pronotum without row of deep punctures 31
31. Elytral punctation dual, with series of smaller and larger punctures .... *P. castaneus* Lea
— Elytral punctation not dual 32
32. Antennal segments 4–7 slightly compressed, segment 8 distinctly compressed; total length 2.25 mm; Northern Territory .... *P. scabricollis* Lea
— Antennal segments 4–7 moniliform, segment 8 only slightly compressed; total length 3 mm; South Australia .... *P. ovipennis* Lea
33. Pronotum without median fovea near the base (Fig. 28); antennae 3-segmented, the last segment forming a solid, cylindrical club without any trace of sutures (Fig. 15) .... *E. formicarum* Pascoe
— Pronotum with median fovea near the base; antennae 7-segmented, or 3-segmented with the last segment flattened (Fig. 20) 34
34. Antennae 7-segmented, the last 5 segments not fused together .... *E. clavatus* Mjöberg
— Antennae 3-segmented with the club flattened and apparently consisting of 5 fused segments (Fig. 20) .... *E. pascoei* Westwood

Notes on the Genera

Diplocotes.—In most of the species, the clypeus is simple and only slightly convex (Fig. 1), but in others it is more tumid and may have a short carina above (Fig. 4). In *kingi* (Fig. 8) it is somewhat constricted in the middle, and in *carinaticeps* (Fig. 7) a narrow, median ridge is formed.

The antennae may have from two to eleven segments. The simplest or least modified type of antenna occurs in *famil-*

iaris (Fig. 21); there are 11 segments, most of which are longer than wide, and the last segment is not modified at the apex. In *foveatus, longicornis, metallicus,* and *myrmecophilus,* the antennae are also 11-segmented, but the segments tend to be shorter and the last segment is truncate and pubescent at the apex. In *longicornis* the last segment is very long, and in *intricatus* most of the segments are transverse and several have apical pubescence. In several other species, the penultimate segment is enlarged and longer than the last segment (Fig. 17); these forms may have 11-segmented (*armicollis, foveicollis, howittanus,* and *minutus*), 10-segmented (*strigicollis* and *brevipennis*), or 9-segmented (*similis, apicalis, pilosus,* and *carinaticeps*) antennae. In *kingi* the antennae are 3-segmented, and the last segment is enlarged and strongly flattened, while *cuneiformis* has 2-segmented antennae with the second segment wedge-shaped (Fig. 35). *D. laticornis* presents a problem, since there has been some confusion concerning the number of segments in the antenna. There are apparently 10 segments, and the last nine are strongly flattened (Fig. 19). Mjöberg (1916) states that there are 11 segments and that segment 2 is greatly reduced, as in some species of Paussidae (see Darlington, 1950). After examining carefully the antenna of this species, we cannot agree with Mjöberg on this matter; the apparent second segment is actually a condyle attached to the real segment 2. It is more probable that reduction of segments has taken place at the apex of the antenna.

The simplest type of pronotum in this genus also occurs in *familiaris* (Fig. 32); a transverse, basal impression is present, anterolateral teeth and a median fovea are absent, and trichomes are small and indistinct. Other species may have various combinations of the above characters; *D. strigicollis,* for instance, has sharp anterolateral teeth on the pronotum but lacks a median fovea and trichomes, while in *D. longicornis* (Fig. 31) the teeth are lacking, but the fovea and trichomes are quite distinct. In several species (*brevipennis, armicollis, laticornis, kingi, cuneiformis,* and *carinaticeps*), the pronotum is short and broad, with sharp anterior teeth, a median fovea, and distinct trichomes that are connected with longitudinal grooves on the disc (Figs. 30 and 35). *D. foveicollis* has a similar pronotum, but it is not as short and broad, and the anterior teeth are replaced by tuberculate processes.

The elytra in almost all of the species are bulbous and strongly convex, but in *D. myrmecophilus* they are somewhat flattened. In some species there may be several distinct pits at the bases of the elytra, but these are absent in *foveicollis, armicollis, laticornis, kingi, cuneiformis,* and *carinaticeps.*

Polyplocotes.—The clypeal structure in this genus does not vary considerably, but the shape of the clypeal plate and the extent of the apical cleft differ among the species. In *P. perforatus* there is a lateral perforation beneath the clypeal plate.

The antennae are less variable than in *Diplocotes,* and in most of the species they are 9-segmented with the penultimate segment enlarged (Fig. 18). In *P. longipes* most of the antennal segments are elongate, but in *longicollis, nitidus* and several others they are more robust and the last two are somewhat flattened. The antennae of *sulcifrons* (Fig. 22) are very similar, but there are only six segments. In *P. dolichognathus, P. antennalis,* and *P. cremastogastri* most of the antennal segments are flattened, as in *Diplocotes laticornis* (Fig. 19); in the first species the antennae are 10-segmented, while *antennalis* and *cremastogastri* have 9-segmented antennae.

Most of the species have a simple type of pronotum with a weak basal impression and small trichomes usually not visible from above (Fig. 34). In *P. perforatus* (Fig. 33) the basal impression is absent and the pronotum is narrowed anteriorly; basolateral trichomes are absent, but there are tufts of yellow hairs along the anterior

edge of the pronotum that may represent lateral trichomes that have been displaced.

Ectrephes.—The species in this genus fall into two groups: *E. formicarum* with a simple pronotal disc (Fig. 28) and the terminal segment of the 3-segmented antenna forming a solid, cylindrical club (Fig. 15), and the other two species (*pascoei* and *clavatus*) with a foveate pronotum and the distal antennal segments strongly flattened and variously fused so that the total number of segments is three (Fig. 20) or seven. It is interesting that these species and also *D. kingi* and *D. cuneiformis* have the tibiae enlarged and angulate proximally.

In the past there has been some confusion concerning the names *Ectrephes* and *Monectrephes.* Mjöberg (1916) divided *Ectrephes* into three genera: the original genus *Ectrephes* with its type *E. formicarum* Pascoe, *Mesectrephes* for *E. kingi* Westwood, and *Monectrephes* for *E. pascoei* Westwood. He also described another species, *E. clavatus,* which he referred to *Monectrephes.* Then in discussions of the various genera he continually transposed the names. He mentions that *Ectrephes* is the least differentiated, having the last segments of the antennae more or less joined together and the penultimate segment excavated at the apex and receiving the last (this is a description of *E. pascoei,* not *E. formicarum*). He then states that in *Monectrephes* there are only three joints, the last one being very long and forming a solid club (this refers to *E. formicarum*). This type of transposition occurs in several other places, including the key to the genera. Because of this, later authors (Lea, 1917; Pic, 1929) synonymized *Monectrephes* with *Ectrephes,* assuming that both were based on the same species, *E. formicarum.* In Mjöberg's first discussion of the genera, however, *E. formicarum* was referred to as the type of *Ectrephes* and *E. pascoei* was definitely placed in *Monectrephes.* The latter species is designated as type of *Monectrephes* in the catalogue below. We think that Mjöberg had not misidentified the species but had merely transposed the names. If this hypothesis is acceptable, then *Ectrephes* and *Monectrephes* are based on different species and are not objective synonyms, although they are here considered to be subjective synonyms.

ORIGIN AND EVOLUTION OF MYRMECOPHILY IN THE PTINIDAE

Habitats and Food Habits

Most ptinid beetles are scavengers, and they are known to feed on a wide variety of animal and plant substances. The major kinds of habitats from which ptinids have been recorded are: (1) under bark and in decomposing wood, (2) in caves, (3) in the nests of birds and mammals, (4) in the nests of other insects, and (5) in association with various stored products of man. Because of the economic importance of these beetles, there have been several attempts to summarize the information pertaining to their biology; most of the following discussion is based on papers of Hinton (1941), Linsley (1944), and Howe (1959), all of which contain extensive bibliographies.

In Europe, *Ptinus subpilosus* Sturm, *P. palliatus* Perris, and *P. lichenum* Marsham are commonly collected under bark and in decaying wood. According to Crowson (1962), *P. subpilosus* occurs chiefly on old, mossy, partly dead oaks in Scotland, and the larvae have been found in decaying oak wood. The larva of *P. lichenum* has been reported to bore into dry fig wood (Howe, 1959), but no ptinid is known to utilize wood as food. Reitter (1911) records *P. subpilosus* from dry moss, *P. pilosus* Müller from old deciduous trees, and *P. sexpunctatus* Panzer from beneath pine and maple bark, and Linsley (1944) lists four other records from European literature. In North America, two species of *Ptinus* were collected by beating live oaks in southern California (Fall, 1901), a specimen of *P. bimaculatus* Melsheimer was taken in Spanish moss in Louisiana, and specimens of *P. fur* Linnaeus have been found in associa-

tion with *Pinus* in New England. Although the beetles may be feeding on rotten wood, it is also possible that they utilize insect remains or other organic debris.

Several ptinids have been recorded from caves, where they usually feed on bat guano or other mammal excrement. Brown (1959) described *Pseudeurostus kelleri* and *Niptus abditus* from specimens taken in caves in Utah, and four other species have been collected in caves in Europe and northern Africa (Howe, 1959). An undescribed *Niptus* was found feeding on raccoon scat in a Texas cave (Reddell, 1966). Although mammal dung appears to be an important food source in all the more sheltered habitats mentioned here, ptinid beetles have never been found in cattle droppings and are rarely collected in other kinds of dung in open places. One notable exception is given by Andrews (1967), who collected two Central American *Ptinus* in coati (*Nasua narica*) scat on exposed surfaces in a dry tropical forest.

The most important natural habitats of the Ptinidae are the nests of mammals, birds, bees, wasps, and ants. Linsley (1944) and Howe (1959) list 11 species of ptinids from mammal nests, 17 species from bird nests, and 12 species from the nests of hymenopterous insects. The actual type of food utilized varies with the kind of nest, but here again excrement is probably an important food item, along with dead insects, hair or feathers, pollen, and possibly living larvae. According to Linsley and MacSwain (1941), *Ptinus californicus* Pic, which lives in the nests of *Osmia*, does not attack the bee larva but may cause its death indirectly through competition for pollen. *P. sexpunctatus*, on the other hand, feeds on healthy larvae of *P. fur* (Howe, 1959). A number of economically important species, including *Niptus hololeucus* (Faldermann), commonly feed on rat and mouse feces, and the infestation of warehouses and mills by these beetles may be associated with the presence of rodents.

The biology of ptinids attacking stored products has been adequately covered by Howe and others. Hinton (1941) lists 21 economically important species, and Howe (1959) has made detailed studies of 14 of these. Some of the many items on which ptinids have been reported to feed are: wheat, flour, rye, cereals, bread, hay, corn, ginger, nutmeg, cacao, opium, fish meal, sugar, pepper, tallow, wool, tobacco, paste, dried mushrooms, dried fruits, rubber, leather, plant and insect collections, and books. Although some of these records are suspect, the total range of food items is still very great.

Biology of the Myrmecophilous Species

Very little is known about the habits of inquilinous ptinids, and the present discussion is based partly on knowledge of the food habits of non-myrmecophilous species, facts concerning the distributions and nesting habits of host ants, interpretation of structural adaptations in the myrmecophilous Ptinidae, and information on the behavior of other myrmecophiles which have evolved analogous structural features.

Most, if not all, of the myrmecophilous ptinids would be considered symphiles or true guests, according to the ecological classification proposed by Wasmann (1898). Most of the species have the characteristic "symphilic features" mentioned by Donisthorpe (1927), Wheeler (1928), and Park (1964): smooth and shiny, black or reddish integument, reduced mouthparts, trichomes, and antennal modifications. Behavioral observations indicate that some species, at least, are tolerated and even protected by the ant colony. Clark (1923) noted that specimens of *Enasiba tristis* and *E. conifer* in an observation nest containing an active colony of *Iridomyrmex conifer* "seemed to be on friendly terms with the ants, and, during the three months' confinement were never interfered with, but were allowed to move freely through the various chambers, including the nurseries which always contained a large number of larvae and pupae of the ants." He further observed that "one,

and sometimes two ants were seen to attach themselves to the antennae, and appeared to be getting great satisfaction by nibbling and licking the apical joints, stroking the beetle meanwhile with their antennae. None of the ants were seen to attach themselves to the fascicles on the prothorax." The following comments were made about *Diplocotidus formicola* by Wasmann and Brauns (1925): "The species is not only tolerated by the ants but seems to be treated as a true guest like most of the Paussidae. When opening the ants' nest I have often observed that the *Plagiolepis* [*Anoplolepis* spp.] grasped the beetles and carried them away into security. . . . The behavior of the beetle is unconcerned. It runs carelessly in the thickest throng of the otherwise vicious and carnivorous *Plagiolepis* and can be observed sitting in copula in the crowd of ants." Although there is no other direct evidence pertaining to the biology of myrmecophilous ptinids, studies of other inquilinous beetles may shed some light on certain features, such as the functions of trichomes and antennal modifications, feeding and means of dispersal.

The tufts of hairs or trichomes on the prothorax, elytra, or abdomen of myrmecophiles secrete some substance which is imbibed by ants. The licking of trichomes by ants has been observed for a number of beetle groups, including the "lomechusine" Staphylinidae (Wasmann, 1920; Wheeler, 1928), the clavigerine Pselaphidae (Donisthorpe, 1927; Park, 1964), and the Paussidae (Reichensperger, 1948). In a detailed anatomical and histological study, Mou (1938) demonstrated that the trichomes of the Paussidae are definitely glandular, producing a secretion which evaporates slowly, leaving a greasy residue which is difficult to dissolve in alcohol but easily soluble in ethyl acetate. Park (1964) made the following comment on the behavior of ants which had been feeding on clavigerine trichomes: ". . . on several occasions, I have observed the workers to be so overwhelmed by this trichome stimulant that they become temporarily disoriented and less sure of their footing." The predaceous reduviid bug *Ptilocerus ochraceus* Montandon produces a secretion which not only attracts ants but narcotizes them as well, enabling the bug to penetrate and feed on the paralyzed prey (Wheeler, 1928; Donisthorpe, 1927).

According to Wheeler (1928) the modified antennae of some myrmecophiles are adapted to stroking the ant host, or function as handles for the ants to carry the beetles about in the nests. According to Mou (1938) and Janssens (1949), however, the antennae of paussids are definitely glandular and probably serve the same function as the trichomes on the prothorax. The observations on *Enasiba* mentioned above indicate that this is also true in some Ptinidae. Darlington (1950) stresses the apparent loss of the tactile function in paussid antennae, as suggested by the reduction or loss of the pedicel and the associated Johnston's organ.

Since most other ptinids are scavengers, it is unlikely that the inquilinous forms feed on ant larvae as do staphylinids and paussids. The most probable sources of food are excrement, dead ants, and the remains of prey. In some of the Ptinidae, however, the mouthparts are reduced, indicating that they may be fed regurgitated food by the ants. Free-living ptinids, such as *Ptinus fur* (Figs. 11 and 14) have normal chewing mandibles and well-developed maxillae with two distinct lobes. In *Diplocotes familiaris* both structures are somewhat reduced, and in *Ectrephes formicarum* the mandible is narrow and scoop-like (Fig. 13) and the maxilla is highly reduced (Fig. 12). Reduction of mouthparts and feeding by ants is a common feature in other symphiles. According to Donisthorpe (1927), *Artemeles* (Staphylinidae) elicits food from worker ants by tapping with its antennae, but can survive on ant larvae and dead insects as well. Park (1964) described an individual of *Adranes lecontei* Brendel being fed regurgitated food by one worker

while two more ants were licking its trichomes.

Since many species of Ptinidae, including almost all of the inquilines, are wingless in both sexes, the means of dispersal in these insects is difficult to explain. A clue may be found in observations made on certain clavigerine Pselaphidae, which are also wingless. *Adranes lecontei* Brendel is known to ride the gaster of worker ants and has been observed to be carried in this manner for as long as ninety minutes (Park, 1964). *Claviger testaceus* Preyssler may attach itself to winged females and males of its host, and Donisthorpe (1927) noted that two specimens of *Claviger longicornis* Müller frequently sat for hours on the gaster of an *Acanthomyops fuliginosus* queen. It is quite possible, then, that a number of myrmecophilous insects may be transported to new nests by queen ants.

The small number of available host records makes it impossible at present to determine the extent to which particular ptinids are restricted to one species or one group of ants. In the New World, *Gnostus* is known only from *Crematogaster* nests and *Fabrasia* is associated only with *Camponotus*, but in Australia the situation is more complex. Many of the Australian forms are associated with species of *Iridomyrmex*, but several have been found in *Crematogaster* and *Rhytidoponera* nests. Seven different ptinids have been taken in the nests of *Iridomyrmex conifer* Forel, and some have been associated with as many as three ant species. *Iridomyrmex conifer* occurs in the dry southwestern part of Australia, and it builds large, conical mounds of twigs and leaves. Most of the Australian ant hosts are ground nesting, while *Camponotus* and *Crematogaster* in the New World usually build nests off the ground in rotten wood, twigs, and vines.

Origin of Myrmecophily

According to Crowson (1955), the Ptinidae have probably evolved from an anobiid-like ancestor resembling the genus *Hedobia*, with the loss of the wood-boring habit being the most important factor involved in the divergence of the group. He considers the ptinid genus *Xylodes* to be intermediate between *Hedobia* and a primitive *Ptinus*, such as *P. palliatus*. Assuming that there was a shift from xylophagy to general scavenging, the ancestral forms may have first fed on rotten wood mixed with excrement and insect remains. Some extant species have retained this habit, as noted above. Two independent trends must then have taken place: (1) the movement away from the arboreal or woody habitat, and (2) the increased utilization of animal by-products, including stored food, feces, and carrion. It is not surprising that many species came to inhabit the nests of birds, mammals, and insects, since the greatest accumulations of suitable food items would be found in these habitats. Also, the Ptinidae have become particularly successful in arid regions where nests of various kinds provide one of the few habitats in which sufficient moisture is available for the completion of the life cycle. Howe (1959) stresses the fact that ptinids require "drinking" water, which would be present in nests in the form of urine, moist excrement, honey, or other fluids. As mentioned above, the species which invaded warehouses and mills were probably first associated with rats and mice. From these general nest scavengers evolved the depredators, such as *Ptinus californicus* and *P. sexpunctatus*, and the myrmecophiles.

The invasion of the nests of social insects, such as ants, presents a problem to the potential inquiline, who must overcome the strong defenses of the colony. Unlike the myrmecophilous Staphylinidae, the slow-moving ptinids certainly have never been active predators, and the first species to penetrate ant colonies were probably indifferently tolerated forms or synoeketes, in the terminology of Wasmann (1898). *Ptinus subpilosus* is a living species which may be a synoekete, since it lacks trichomes or other symphilic features but appears to

have invaded successfully the nests of *Acanthomyops* in Europe. These secretive forms may be able to survive in the nest by occupying abandoned chambers or by feigning death when disturbed (letisimulation). The latter type of behavior, which has been discussed by Park (1964) for the Pselaphidae, may have been very important in the initial adjustment to the ant society. It is likely that beetles exhibiting letisimulation would be ignored by worker ants or possibly carried off with the debris. It is also possible that certain structural features of the Ptinidae have preadapted them for myrmecophilous existence. All ptinids are relatively small and compact beetles with a heavy cuticle. The head is declined and the prosternum shortened, so that the mouthparts and antennae may be hidden beneath the body. If a beetle were to be attacked, the compact form and thick cuticle might provide sufficient protection, but this would not be necessary for survival if enough of the population avoided encounters with the ants. Once this initial adjustment was made, the inquiline would be provided with a compatible environment (especially in arid regions), an abundant food supply, and the protection of the colony. Selection would favor the subsequent evolution of features either that would improve the defenses of the inquiline or allow it to become integrated into the ant society as a protected symphile.

There is little doubt that in several groups, such as the Ptinidae, Paussidae, and Pselaphidae, the evolution of true symphily has been associated with the development of glandular structures, such as trichomes, but the functions of these glands and the steps leading to their development are far from being clearly understood. It is known that ants may imbibe the secretions and that insects possessing trichomes are often protected and fed by ants, but the relationships between symphiles and their hosts have never been studied in detail. Unlike aphids and coccids, these insects are not tended in groups outside the nest, nor do they supply a significant amount of nutriment to the colony. Symphiles are known to occur in small numbers throughout the active portions of the nest and they appear to be accepted as part of the colony. It may be argued that any "foreign" insect producing secretions which stimulate the ants to feed would be devoured rather than protected, but several factors may prevent this. First, it has been assumed that the initial invaders have penetrated the nest in the manner discussed above and have thus taken on the colony odor. Second, most of these symphiles resemble ants and some of them, at least, exhibit antlike behavior. Third, the aggressive behavior of a foraging or defending worker is unlike that of an ant within the nest, where a common activity is the exchange of regurgitated food or secretions (trophallaxis). If a myrmecophile elicits no defensive response from the ants, and if trophallactic exchange is a common pattern among individuals within the nest, it is conceivable that the development of attractive secretions by an inquiline might lead directly to a situation in which the insect is not only protected but also fed by the ants.

In the preceding discussion it is assumed that trichomes developed in beetles which already had invaded successfully the nests of ants. It is also possible that these glands were a necessary prerequisite to the invasion of nests. Cazier and Mortenson (1965) suggest that in the scarabaeid beetle *Cremastocheilus* trichomes may serve to attract ants to the beetles which are then carried into the nest as items of food. A third alternative is that trichomes evolved independently and serve no necessary function in myrmecophily. We think that the occurrence of these structures in so many unrelated myrmecophiles makes this last suggestion improbable.

As mentioned above, myrmecophily in the Ptinidae probably originated several times. *Myrmecoptinus buttcli*, a winged species associated with *Crematogaster* in

the forests of Southeast Asia, is the least modified of the inquilines and may have evolved recently from non-myrmecophilous forms. We have suggested (Lawrence and Reichardt, 1966a) that the two New World genera, *Gnostus* and *Fabrasia*, evolved directly and independently from early *Ptinus*-like ancestors. The species in both groups are highly modified symphiles, but they have retained their wings and are associated with arboreal or wood-nesting ants in the American tropics. The South African *Diplocotidus* and the Australian ectrephines are all wingless, and most of them occur with ground-nesting ants in open, arid or semi-arid regions. These two groups may have evolved from ancestors which had already left the ancestral forest habitat and were associated with ground debris or mammal burrows in dry areas. *Diplocotidus formicola* is a true symphile, judging from the observations of Wasmann and Brauns (1925), but it has not evolved some of the more obvious antennal and pronotal modifications found in the Australian forms. The ectrephines are the most diverse and numerous of the myrmecophilous ptinids, but they have almost certainly evolved from one or possibly two related forms; all are probably symphiles, but the degree of structural modification varies considerably.

Only six species of myrmecophilous ptinids occur in the Neotropical region, while 35 species are known from Australia. Furthermore, the New World fauna consists of three closely related species in each of the two genera, while the Australian fauna is so diverse that the species were formerly placed in 14 genera. Certainly the habitat diversity of South America exceeds that of Australia, and the ant faunas of the two areas are comparable. The following factors are likely to have been responsible. First, the Ptinidae in general seem to be more successful in arid and semi-arid regions than in humid, tropical ones, and most of the Australian ectrephines inhabit the drier parts of the continent. Second, the Australian inquilines are all wingless (which may be related to water conservation in dry areas), while the New World species are winged. The lack of wings will obviously reduce the rate of gene exchange between populations. If, as suggested above, the wingless myrmecophile must attach itself to a new queen, then the probability of outbreeding will be very low. Finally, the Australian ant fauna contains a large number of ground-nesting species, such as *Iridomyrmex conifer*, which build mounds and have relatively large and permanent colonies. The South American ants, on the whole, have smaller and less permanent colonies. These *Iridomyrmex* nests provide a suitable environment for the build-up of inquiline populations, which, because of difficulties of dispersal, may be isolated from other such populations for long periods of time. Such conditions would favor the evolution of a diverse myrmecophilous fauna.

Evolutionary Trends

In examining the various modifications of myrmecophilous ptinids, we may distinguish between those unique to inquilines and those found in other Ptinidae as well. The former group would include: elongation of clypeus and labrum, reduction of mouthparts, enlargement, flattening, and fusion of antennal segments, formation of glandular structures on antennae, pronotum, elytra, and hind legs, changes in shape of tibiae, and loss or extreme reduction of hairs and scales over most of the body surface. The following would fall into the latter group: reduction of eyes, declination of head, formation of deep antennal fossae, loss of antennal segments, formation of grooves and pits on pronotum, loss of hindwing, reduction or loss of scutellum and elytral humeri, reduction of metasternum, and lateral movement and change in shape of hind coxae.

The loss of the hindwings (with the correlated changes in the elytra, scutellum, and metasternum) occurs in various Ptin-

idae, including *Mezium*, *Gibbium*, *Niptus*, and *Trigonogenius*, while some of the myrmecophiles have fully developed wings (*Gnostus* and *Fabrasia*). Since most of the wingless ptinids occur in drier areas or in stored products, it is possible that the loss of wings is associated with water conservation.

Changes in the shape of the clypeus and labrum are unique to the myrmecophilous species, and may serve to protect the mouthparts. In some of the highly modified forms, such as *Ectrephes*, the concave inner surface of the labrum forms with the hollowed and elongate mandibles a tube which may be used for feeding on liquids supplied by the ants. In these same forms, the chewing surface of the mandible is absent and the maxillae are reduced.

Modifications of the legs of these inquilines probably represent three different kinds of adaptations. In *Gnostus*, the tibiae are broad and compressed and may serve as protective shields; very similar structures occur in the paussid genera *Homopterus* and *Cerapterus*. The tibiae of *Ectrephes formicarum* and certain other ectrephines are somewhat bent and angulate; these might be used to cling to ants. The hind tibiae and femora of *Fabrasia* are peculiarly enlarged and bear tufts of yellow hairs; these are probably glandular structures serving the same function as trichomes.

The types and possible functions of pronotal and antennal trichomes have been discussed above. Several different types of glandular systems have evolved in this group, but the diversity is not nearly as great as in the Paussidae (see Darlington, 1950). Perhaps the first structures were small isolated glands scattered on the body surface. A consolidation of these small glands gave rise to more complicated organs, such as trichomes, and to various accessory grooves and pits for the collection of fluid. The fusion of antennal segments would serve to consolidate glandular material and form a storage vesicle as well.

The evolution of antennal types in the Ptinidae is similar in many ways to that occurring in the Paussidae, and a number of convergences can be seen in the two groups. *Protopaussus* has simple antennae like those of *Diplocotes familiaris*, while *Homopterus*, *Cerapterus*, and their relatives have the flattened type of antennae found in *D. laticornis*. *Lebioderus* and *Pentaplatarthrus* have flattened antennae with a reduced number of segments, and in *Ceratoderus* and *Platyrhopalopsis* further fusion and reduction can be seen; this series finds a parallel in *Diplocotes kingi*, *Ectrephes clavatus*, and *E. pascoei* among the ptinids. The club-like antenna found in *E. formicarum* and the genus *Gnostus* is similar to that of some *Paussus*.

CATALOGUE OF THE MYRMECOPHILOUS PTINIDAE

Myrmecoptinus Wasmann

Myrmecoptinus Wasmann, 1916: 206–207. Type species, by monotypy, *Myrmecoptinus butteli* Wasmann.

Included species: 1.

Myrmecoptinus butteli Wasmann

Myrmecoptinus butteli Wasmann, 1916: 207, pl. 4, fig. 20.

Distribution: SUMATRA (Soengei, Bamban).

Host: Crematogaster butteli Forel.

Diplocotidus Peringuey

Diplocotidus Peringuey, 1899: 245. Type species, by monotypy, *Diplocotidus formicola* Peringuey.

Included species: 1.

Diplocotidus formicola Peringuey

Diplocotidus formicola Peringuey, 1899: 245–246, pl. 7, figs. 13, 13a; Wasmann and Brauns, 1925: 112–113.

Distribution: UNION OF SOUTH AFRICA (Prince Albert; Willowmore; Ladysmith; Kimberley).

Hosts: Acantholepis capensis Mayr; *Anoplolepis custodiens* (F. Smith); *Anoplolepis steingroeveri* (Forel).

Gnostus Westwood

Gnostus Westwood, 1855: 90–92; Lawrence and Reichardt, 1966a: 32–34. Type species, by monotypy, *Gnostus formicicola* Westwood.

Included species: 3.

Gnostus formicicola Westwood

Gnostus formicicola Westwood, 1855: 92, pl. 8, figs. 1–21; Lawrence and Reichardt, 1966a: 34, fig. 4.

Distribution: BOLIVIA: LA PAZ (Mapiri); BRAZIL: PARÁ (Santarém; Villa Nova); AMAZONAS (São Paulo de Olivença); MATO GROSSO (Utiariti).

Hosts: Crematogaster victima F. Smith; *Crematogaster* sp. (near *brasiliensis* Mayr).

Gnostus floridanus Blatchley

Gnostus floridanus Blatchley, 1930: 111–112, fig. 1; Lawrence and Reichardt, 1966a: 37, figs. 1, 2, 5, 13, 14.

Distribution: BAHAMAS (Clifton Point, New Providence); FLORIDA (Dunedin; Plantation Key).

Hosts: Crematogaster ashmeadi Mayr; *Crematogaster sanguinea lucayana* Wheeler.

Gnostus meinerti Wasmann

Gnostus meinerti Wasmann, 1894: 121, 216; Lawrence and Reichardt, 1966a: 35, fig. 3.

Distribution: PANAMA (Barro Colorado Is.; Erwin Is.; Gatun Lake); VENEZUELA: CARABOBO (Trincheras, near Valencia).

Host: Crematogaster limata dextella Santschi.

Fabrasia Martinez and Viana

Fabia Martinez and Viana, 1964: 8, not Dana, 1851. Type species, by original designation, *Fabia alvarengai* Martinez and Viana.

Fabrasia Martinez and Viana, 1965: 18; Lawrence and Reichardt, 1966a: 37–40.

Included species: 3.

Fabrasia alvarengai (Martinez and Viana)

Fabia alvarengai Martinez and Viana, 1964: 9, figs. 1–3.

Fabrasia alvarengai (Martinez and Viana), 1965: 18; Lawrence and Reichardt, 1966a: 41.

Distribution: BRAZIL: RIO GRANDE DO NORTE (Natal).

Host: Unknown.

Fabrasia borgmeieri Lawrence and Reichardt

Fabrasia borgmeieri Lawrence and Reichardt, 1966a: 41–42, figs. 6–7.

Distribution: BRAZIL: GOIÁS (Campinas); MINAS GERAIS (Poços de Caldas).

Host: Camponotus (Myrmothrix) renggeri Emery; *Camponotus (Myrmobrachys) senex* (F. Smith).

Fabrasia wheeleri Lawrence and Reichardt

Fabrasia wheeleri Lawrence and Reichardt, 1966a: 42–44, figs. 8–12.

Distribution: COLOMBIA: MAGDALENA (Sevilla); MEXICO: OAXACA (6.3 mi. W Tehuantepec).

Host: Camponotus (Myrmothrix) bugnioni Forel.

Diplocotes Westwood

Diplocotes Westwood, 1869: 317. Type species, by monotypy, *Diplocotes howittanus* Westwood.

Diphobia Olliff, 1886: 837–838. Type species, by monotypy, *Diphobia familiaris* Olliff. NEW SYNONYMY.

Paussoptinus Lea, 1905: 381. Type species, by monotypy, *Paussoptinus laticornis* Lea. NEW SYNONYMY.

Decemplocotes Mjöberg, 1916: 2; Lea, 1917: 146 (proposed synonymy with *Diplocotes*). Type species, by present designation, *Diplocotes strigicollis* Lea.

Mesectrephes Mjöberg, 1916: 3. Type species, by monotypy, *Ectrephes kingi* Westwood. NEW SYNONYMY.

Bitrephes Oke, 1926: 291; Oke, 1928: 27. Type species, by monotypy, *Bitrephes cuneiformis* Oke. NEW SYNONYMY.

Falsoectrephes Pic, 1929: 35. Type species, by monotypy, *Ectrephes kingi* Westwood. NEW SYNONYMY.

Included species: 19.

Diplocotes apicalis (Oke), NEW COMBINATION

Polyplocotes apicalis Oke, 1928: 26.

Distribution: AUSTRALIA: VICTORIA (Hattah).

Host: Iridomyrmex sp.

Diplocotes armicollis Lea

Diplocotes armicollis Lea, 1910: 219–220, figs. 25–26.

Distribution: AUSTRALIA: SOUTH AUSTRALIA (Adelaide).
Host: Unknown. Collected under bark with ants.

Diplocotes brevipennis (Pic)

Paussoptinus brevipennis Pic, 1909: 215; Lea, 1910: 223.
Decemplocotes brevipennis, – Mjöberg, 1916: 6, fig. 6.
Diplocotes brevipennis, – Lea, 1917: 146.
Diplocotes decemarticulatus Lea, 1910: 220–221, fig. 57; Lea, 1917: 146 (syn.).

Distribution: AUSTRALIA: WESTERN AUSTRALIA (Geraldton; Moora).
Host: Unknown.

Diplocotes carinaticeps (Lea), NEW COMBINATION

Polyplocotes carinaticeps Lea, 1919: 254–255, pl. 25, fig. 39; Zeck, 1920: 246, pl. 19, fig. 3; Oke, 1928: 27.

Distribution: AUSTRALIA: VICTORIA (Hattah); WESTERN AUSTRALIA (Swan River).
Hosts: Crematogaster laeviceps F. Smith; *Iridomyrmex conifer* Forel.

Diplocotes cuneiformis (Oke), NEW COMBINATION

Bitrephes cuneiformis Oke, 1926: 291; Oke, 1928: 27–28.

Distribution: AUSTRALIA: VICTORIA (Lake Hattah).
Host: Iridomyrmex rufoniger (Lowne).

Diplocotes familiaris (Olliff), NEW COMBINATION

Diphobia familiaris Olliff, 1886: 838; Lea, 1905: 381; Lea, 1910: 223.
Diplocotes niger Poll, 1886: 238; Blackburn, 1892: 300 (syn.).

Distribution: AUSTRALIA: SOUTH AUSTRALIA (Adelaide); VICTORIA (Kiata).
Hosts: Iridomyrmex nitidus Mayr; *Iridomyrmex nitidiceps* Andre; *Rhytidoponera metallica* (F. Smith).

Diplocotes foveatus (Lea), NEW COMBINATION

Diphobia foveata Lea, 1917: 154–155.

Distribution: AUSTRALIA: QUEENSLAND (Townsville).
Host: Unknown.

Diplocotes foveicollis Olliff

Diplocotes foveicollis Olliff, 1886: 839–840; Lea, 1910: 219; Lea, 1917: 149; Lea, 1919: 257; Clark, 1921: 103.

Distribution: AUSTRALIA: NEW SOUTH WALES; SOUTH AUSTRALIA (Lucindale); WESTERN AUSTRALIA (Serpentine River; Perth; Swan River).
Host: Iridomyrmex conifer Forel.

Diplocotes howittanus Westwood

Diplocotes howittanus Westwood, 1869: 317; Westwood, 1874: 103, pl. 3, fig. 6; Lea, 1910: 219; Oke, 1928: 26.

Distribution: AUSTRALIA: SOUTH AUSTRALIA (Gawler, Adelaide); VICTORIA (Grampians).
Host: Unknown. Collected under bark with ants.

Diplocotes intricatus (Lea), NEW COMBINATION

Diphobia intricata Lea, 1917: 155–156.

Distribution: AUSTRALIA: QUEENSLAND (Stewart River).
Hosts: Crematogaster sp.; *Iridomyrmex* sp.

Diplocotes kingi (Westwood), NEW COMBINATION

Ectrephes kingi Westwood, 1869: 316; Westwood, 1874: 104, pl. 3, fig. 2; Lea, 1910: 222; Lea, 1917: 147.
Mesectrephes kingi, – Mjöberg, 1916: 3.
Falsoectrephes kingi, – Pic, 1929: 35.

Distribution: AUSTRALIA: WESTERN AUSTRALIA (Swan River; Mullewa).
Host: Iridomyrmex sp.

Diplocotes laticornis (Lea), NEW COMBINATION

Paussoptinus laticornis Lea, 1905: 382–383, pl. 28, fig. 7; Lea, 1917: 147; Tillyard, 1926: 215, pl. 16, fig. 14.

Distribution: AUSTRALIA: SOUTH AUSTRALIA (Mindarie; Murat Bay; Murray Bridge; Port Lincoln); VICTORIA (Birchip; Bendigo; Sea Lake).

Hosts: Crematogaster laeviceps F. Smith; *Iridomyrmex nitidus* Mayr; *Iridomyrmex* spp.

Diplocotes longicornis (Lea), NEW COMBINATION

Diphobia longicornis Lea, 1919: 256, pl. 25, fig. 40; Zeck, 1920: 245, pl. 19, fig. 4; Clark, 1921: 103.

Distribution: AUSTRALIA: WESTERN AUSTRALIA (Victoria Park; Swan River).

Hosts: Iridomyrmex conifer Forel; *Iridomyrmex* sp.

Diplocotes metallicus (Lea), NEW COMBINATION

Diphobia metallica Lea, 1917: 155.

Distribution: AUSTRALIA: QUEENSLAND (Stewart River).

Host: Iridomyrmex sp.

Diplocotes minutus Oke

Diplocotes minuta Oke, 1928: 26.

Distribution: AUSTRALIA: VICTORIA (Bendigo).

Host: Rhytidoponera sp.

Diplocotes myrmecophilus (Lea), NEW COMBINATION

Diphobia myrmecophila Lea, 1917: 153–154.

Distribution: AUSTRALIA: NORTHERN TERRITORY (Darwin).

Hosts: Oecophylla smaragdina (Fabricius), *Rhytidoponera hilli* Crawley.

Diplocotes pilosus (Mjöberg), NEW COMBINATION

Polyplocotes pilosus Mjöberg, 1916: 11–12, fig. 3.

Distribution: AUSTRALIA: WESTERN AUSTRALIA (Noonkanbah, Kimberley District).

Host: Unknown.

Diplocotes similis (Oke), NEW COMBINATION

Polyplocotes similis Oke, 1928: 27.

Distribution: AUSTRALIA: VICTORIA (Bendigo; Inglewood).

Host: Crematogaster laeviceps F. Smith.

Diplocotes strigicollis Lea

Diplocotes strigicollis Lea, 1910: 221; Lea, 1917: 150.

Decemplocotes strigicollis, – Mjöberg, 1916: 2.

Distribution: AUSTRALIA: SOUTH AUSTRALIA (Adelaide; Port Lincoln).

Host: Iridomyrmex sp.

Polyplocotes Westwood

Polyplocotes Westwood, 1869: 316. Type species, by present designation, *Polyplocotes longicollis* Westwood.

Hexaplocotes Lea, 1906: 224. Type species, by monotypy, *Hexaplocotes sulcifrons* Lea. NEW SYNONYMY.

Leaptinus Mjöberg, 1916: 3; Lea, 1917: 146 (proposed synonymy with *Paussoptinus*). Type species, by monotypy, *Paussoptinus dolichognathus* Lea. NEW SYNONYMY.

Paussoceros Mjöberg, 1916: 13. Type species, by monotypy, *Paussoceros antennalis* Mjöberg. NEW SYNONYMY.

Included species: 11.

Polyplocotes antennalis (Mjöberg), NEW COMBINATION

Paussoceros antennalis Mjöberg, 1916: 13–14, fig. 4.

Distribution: AUSTRALIA: WESTERN AUSTRALIA (Derby, Kimberley District).

Host: Unknown. Collected under bark.

Polyplocotes castaneus Lea

Polyplocotes castaneus Lea, 1912: 75.

Distribution: AUSTRALIA: WESTERN AUSTRALIA (Northwestern Australia).

Host: Unknown.

Polyplocotes cremastogastri (Lea), NEW COMBINATION

Paussoceros cremastogastri Lea, 1917: 153.

Distribution: AUSTRALIA: WESTERN AUSTRALIA (Derby).

Host: Crematogaster sp.

Polyplocotes dolichognathus (Lea), NEW COMBINATION

Paussoptinus dolichognathus Lea, 1912: 76; Lea, 1917: 146.
Leaptinus dolichognathus, – Mjöberg, 1916: 3.

Distribution: AUSTRALIA: SOUTH AUSTRALIA (Killalpanima, Central Australia).
Host: Unknown.

Polyplocotes longicollis Westwood

Polyplocotes longicollis Westwood, 1869: 316; Westwood, 1874: 103, pl. 3, fig. 4; Lea, 1910: 219; Lea, 1917: 147.
?*Polyplocotes nigropiceus* Pic, 1903: 183.

Distribution: AUSTRALIA: WESTERN AUSTRALIA (Cue; Swan River; Sorrento Beach, Perth District).
Host: Iridomyrmex sp.

Polyplocotes longipes Lea

Polyplocotes longipes Lea, 1917: 152–153.

Distribution: AUSTRALIA: WESTERN AUSTRALIA (Derby).
Host: Crematogaster sp.

Polyplocotes nitidus Westwood

Polyplocotes nitidus Westwood, 1869: 316; Westwood, 1874: 103, pl. 3, fig. 5; Lea, 1910: 219.

Distribution: AUSTRALIA: WESTERN AUSTRALIA (Swan River).
Host: Unknown. Collected with ants.

Polyplocotes ovipennis Lea

Polyplocotes ovipennis Lea, 1914: 256–257.

Distribution: AUSTRALIA: SOUTH AUSTRALIA (Lake Callabonna, Central Australia).
Host: Unknown.

Polyplocotes perforatus Lea

Polyplocotes perforatus Lea, 1917: 150–151, pl. 12, figs. 7–8.

Distribution: AUSTRALIA: WESTERN AUSTRALIA (Beverley).
Host: Unknown. Collected in nests of ants.

Polyplocotes scabricollis Lea

Polyplocotes scabricollis Lea, 1917: 151–152.

Distribution: AUSTRALIA: NORTHERN TERRITORY (Stapleton).
Host: Unknown. Collected in ant nest.

Polyplocotes sulcifrons (Lea), NEW COMBINATION

Hexaplocotes sulcifrons Lea, 1906: 224–225, pl. 18, fig. 8; Lea, 1917: 150; Clark, 1921: 104; Tillyard, 1926: 215, pl. 16, fig. 13.

Distribution: AUSTRALIA: WESTERN AUSTRALIA (Beverley; Newcastle; Perth).
Host: Iridomyrmex conifer Forel.

Ectrephes Pascoe

Ectrephes Pascoe, 1866: xvi; Westwood, 1869: 315. Type species, by monotypy, *Ectrephes formicarum* Pascoe.
Anapestus King, 1866: 317; Westwood, 1869: 315 (proposed synonymy with *Ectrephes*). Type species, by monotypy, *Anapestus kreusleri* King (= *Ectrephes formicarum* Pascoe).
Monectrephes Mjöberg, 1916: 3; Lea, 1917: 145 (proposed synonymy with *Ectrephes*). Type species, by present designation, *Ectrephes pascoei* Westwood.
Pseudectrephes Pic, 1929: 35 (proposed as a subgenus of *Ectrephes*); Schenkling, 1935: 4 (raised to rank of genus). Type species, by monotypy, *Ectrephes clavatus* Mjöberg.

Included species: 3.

Ectrephes clavatus Mjöberg

Ectrephes clavatus Mjöberg, 1916: 14, fig. 5.
Ectrephes (*Pseudectrephes*) *clavatus*, –Pic, 1929: 35.

Distribution: AUSTRALIA: WESTERN AUSTRALIA (Swan River).
Host: Iridomyrmex nitidus Mayr.

Ectrephes formicarum Pascoe

Ectrephes formicarum Pascoe, 1866: xvi–xvii; Westwood, 1869: 315; Westwood, 1874: 104, pl. 3, fig. 1; Lea, 1910: 222; Lea, 1919: 256, pl. 25, figs. 41–42; Zeck, 1920: 246, pl. 19, fig. 1; Clark, 1921: 103; Tillyard, 1926: 215, pl. 16, fig. 15.
Anapestus kreusleri King, 1866: 317, pl. 16; Westwood, 1869: 315 (syn.).

Distribution: AUSTRALIA: SOUTH AUSTRALIA; WESTERN AUSTRALIA (Jandakot; Perth; Swan River).
Hosts: Iridomyrmex conifer Forel; *Rhytidoponera metallica* (F. Smith).

Ectrephes pascoei Westwood

Ectrephes pascoei Westwood, 1869: 315–316; Westwood, 1874: 104, pl. 3, fig. 3.
Monectrephes pascoei, – Mjöberg, 1916: 3.

Distribution: AUSTRALIA: WESTERN AUSTRALIA (Swan River).

Host: Unknown.

Enasiba Olliff

Enasiba Olliff, 1886: 838–839. Type species, by monotypy, *Enasiba tristis* Olliff.

Included species: 2.

Enasiba microcera Clark

Enasiba microcera Clark, 1923: 44–46.

Distribution: AUSTRALIA: WESTERN AUSTRALIA (Bunbury; Busselton).

Host: Iridomyrmex conifer Forel.

Enasiba tristis Olliff

Enasiba tristis Olliff, 1886: 839; Lea, 1919: 254, pl. 25, figs. 37–38; Zeck, 1920: 245, pl. 19, fig. 2; Clark, 1921: 103; Clark, 1923: 46; Tillyard, 1926: 215, pl. 16, fig. 12.

Distribution: AUSTRALIA: WESTERN AUSTRALIA (King George's Sound; Perth; Swan River).

Host: Iridomyrmex conifer Forel.

LIST OF ANT HOST SPECIES AND ASSOCIATED INQUILINES

Formicidae	Ptinidae
Ponerinae	
Ectatommini	
Rhytidoponera hilli Crawley	*D. myrmecophilus* (Lea)
R. metallica (F. Smith)	*D. familiaris* (Olliff)
	E. formicarum Pascoe
Rhytidoponera sp.	*D. minutus* Oke
Myrmicinae	
Crematogastrini	
Crematogaster ashmeadi Mayr	*G. floridanus* Blatchley
C. butteli Forel	*M. butteli* Wasmann
C. laeviceps F. Smith	*D. carinaticeps* (Lea)
	D. laticornis (Lea)
	D. similis (Oke)
C. limata dextella Santschi	*G. meinerti* Wasmann
C. sanguinea lucayana Wheeler	*G. floridanus* Blatchley
C. victima F. Smith	*G. formicicola* Westwood
Crematogaster sp.	*G. formicicola* Westwood
	D. intricatus (Lea)
	P. cremastogastri (Lea)
	P. longipes Lea
Dolichoderinae	
Tapinomini	
Iridomyrmex conifer Forel	*D. carinaticeps* (Lea)
	D. foveicollis Olliff
	D. longicornis (Lea)
	P. sulcifrons (Lea)
	E. formicarum Pascoe
	E. microcera Clark
	E. tristis Olliff
I. nitidiceps Andre	*D. familiaris* (Olliff)

I. nitidus Mayr	*D. familiaris* (Olliff)
	D. laticornis (Lea)
	E. clavatus Mjöberg
I. rufoniger (Lowne)	*D. cuneiformis* (Oke)
Iridomyrmex sp.	*D. apicalis* (Oke)
	D. intricatus (Lea)
	D. kingi (Westwood)
	D. laticornis (Lea)
	D. longicornis (Lea)
	D. metallicus (Lea)
	D. strigicollis Lea
	P. longicollis Westwood
Formicinae	
Plagiolepidini	
Acantholepis capensis Mayr	*D. formicola* Peringuey
Anoplolepis custodiens (F. Smith)	*D. formicola* Peringuey
A. steingroeveri (Forel)	*D. formicola* Peringuey
Oecophyllini	
Oecophylla smaragdina (Fabricius)	*D. myrmecophilus* (Lea)
Camponotini	
Camponotus (*Myrmobrachys*) *senex* (F. Smith)	*F. borgmeieri* Lawrence and Reichardt
C. (*Myrmothrix*) *bugnioni* Forel	*F. wheeleri* Lawrence and Reichardt
C. (*Myrmothrix*) *renggeri* Emery	*F. borgmeieri* Lawrence and Reichardt

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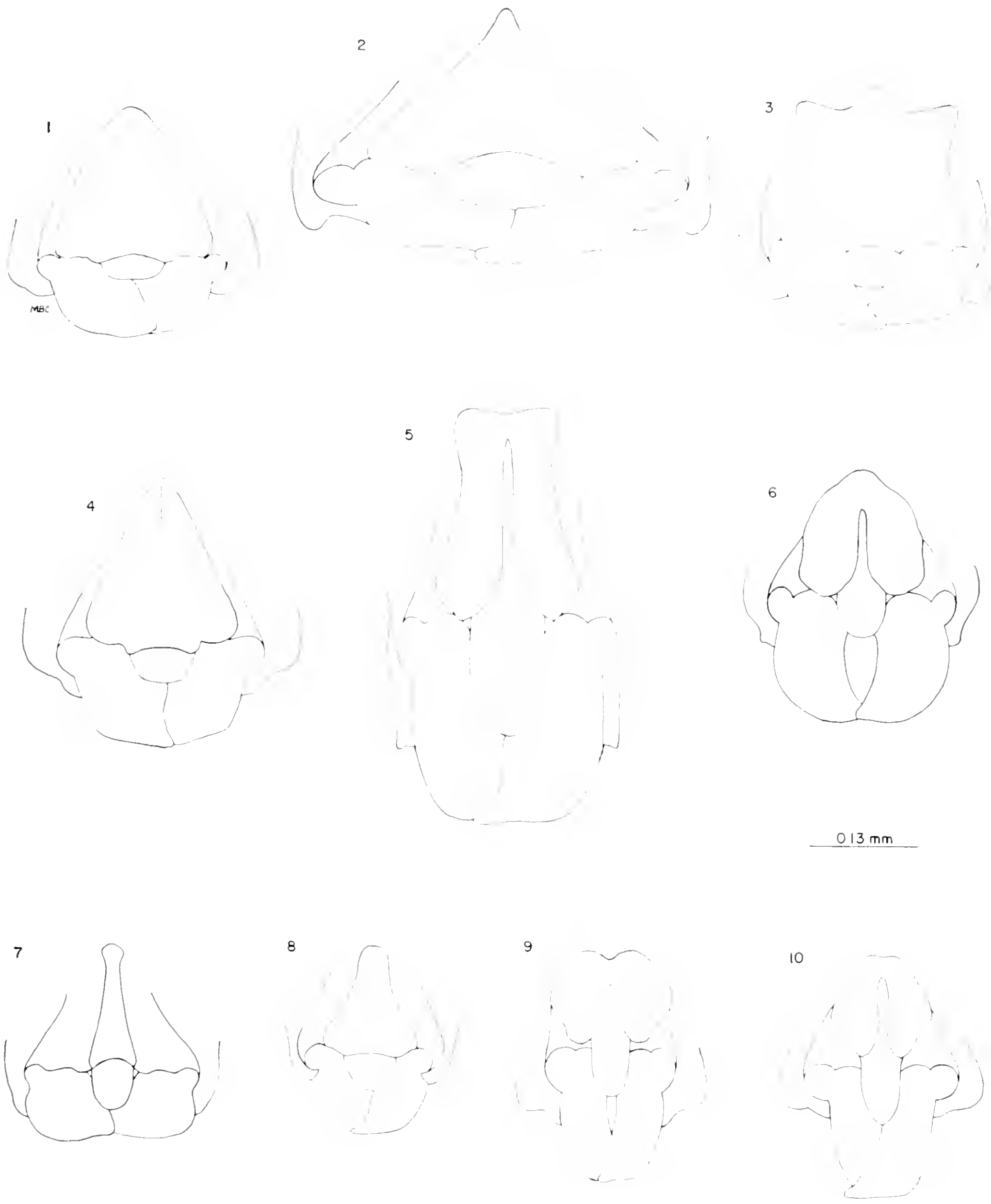

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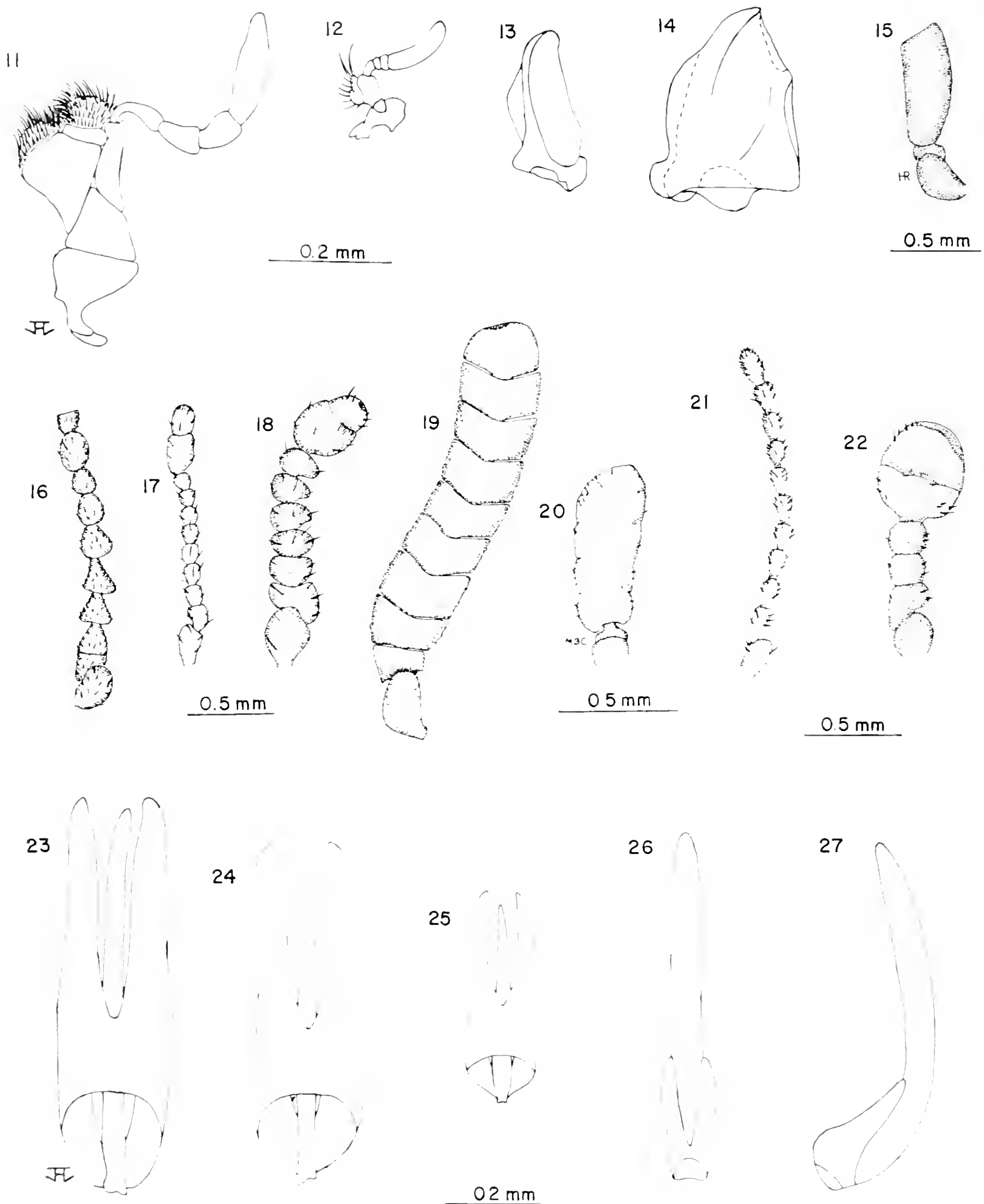

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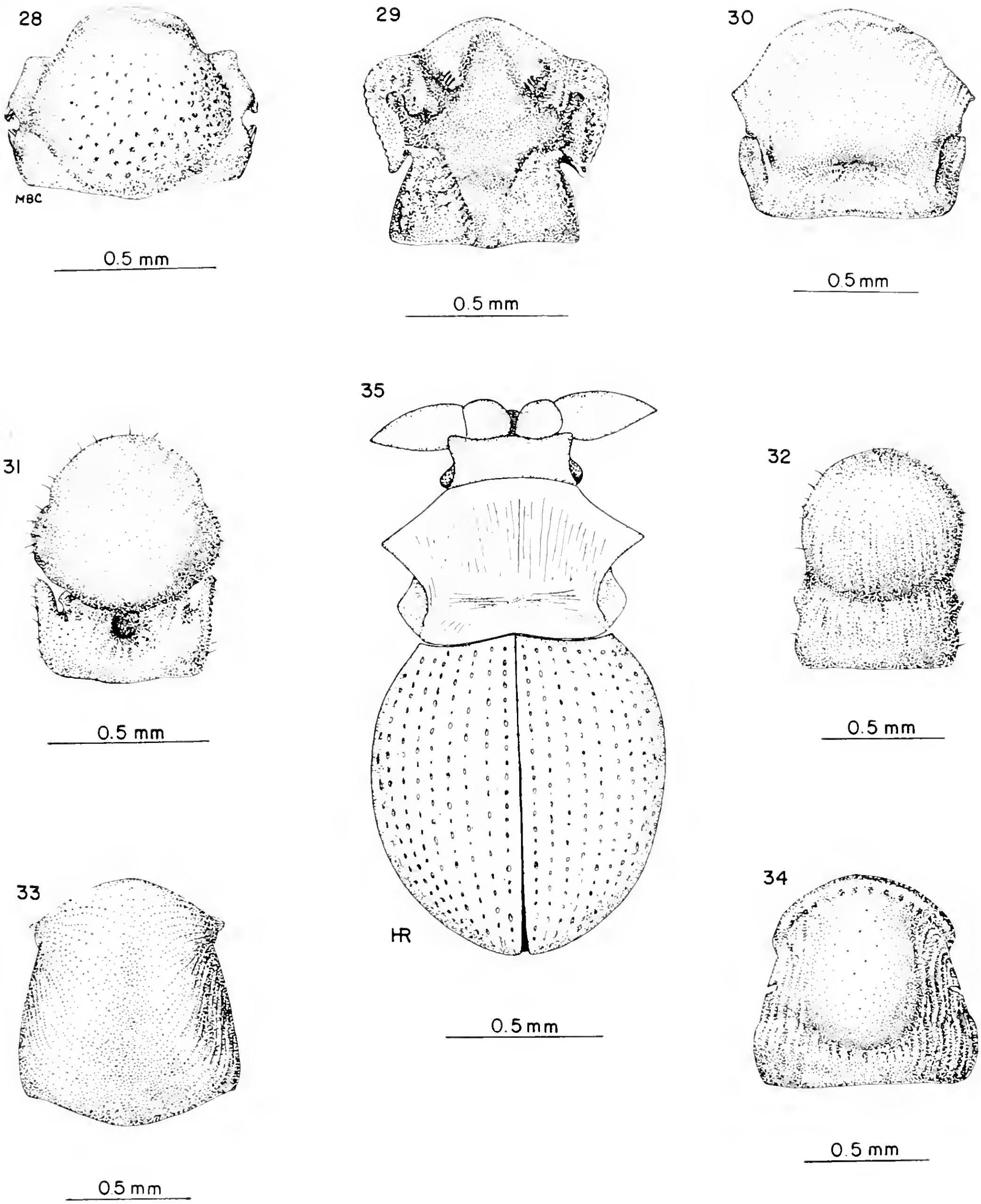

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Host Relationships in North American Fungus-Feeding Moths (Oecophoridae, Oinophilidae, Tineidae)

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HOST RELATIONSHIPS IN NORTH AMERICAN FUNGUS-FEEDING MOTHS (OECOPHORIDAE, OINOPHILIDAE, TINEIDAE)

JOHN F. LAWRENCE AND JERRY A. POWELL[1,2]

ABSTRACT

Feeding habits and habitat preferences are discussed for 19 species of North American Microlepidoptera known to occur in wood-rotting fungi. A brief section on host fungi and the nature of the fungus substrate is followed by a general discussion of host ranges. Detailed biological information is included under each species. *Oinophila v-flava* and members of the Oecophoridae are considered to be general scavengers utilizing fungi occasionally, while the Tineidae include obligate fungus-feeders, occurring mainly in Polyporaceae. Among the Tineidae, some species (*Morophaga cryptophori*) appear to be host-specific, while others (*Nemapogon defectellus*) are ecologically restricted but utilize a number of host fungi. Certain fungus species, such as *Polyporus gilvus* and *P. munzii*, are frequently inhabited by tineids, while *P. versicolor* and certain others serve only as incidental hosts.

INTRODUCTION

A fungus-feeding habit has long been recognized for certain Microlepidoptera, particularly Tineidae. Information about host relationships has been based mainly on European species, and knowledge of the feeding habits of North American species has lagged far behind that of their Palaearctic counterparts. Forbes (1923), for example, gives only a few unidentified host records for fungus-feeding tineids of the northeastern United States, and no fungus associations are given for Oecophoridae. There have been few subsequent reports to fill out this gap in our knowledge. In contrast, fungus hosts are known for a number of British oecophorids (e.g., Meyrick, 1895), and numerous rearing records are available for many of the European fungus-feeding tineids (Hinton, 1956; Petersen, 1957, 1958; Zagulajev, 1964).

In the course of a rearing program for insects, particularly Coleoptera, associated with Polyporaceae and other wood-rotting fungi, during 1960-1963, a number of tineids were reared from various polypores collected in Oregon, California, and Arizona. Although subsequent collections were made especially to obtain information on the moths, many of the records given below are by-products of a survey for Ciidae and other fungus-inhabiting Coleoptera. Consequently, owing to the rearing methods, moths were obtained primarily when nearly mature larvae were incidentally taken with the fungus sample. As a result, many of the collections produced only one or a few individuals, creating problems in the identification of the moths.

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Although many European species in these moth groups have been reared on a number of occasions, reports on these have often included only vague host identifications (i.e., "wood fungus," "fungus on oak," "bred from Polyporus"), and no effort has been made by previous workers to eliminate doubtful records or to analyze host ranges for individual moth species. During the present study we have stressed this aspect of the biology. Since there have been very few reports on North American species, there are no literature records that we have had to consider suspect.

All of the moths involved in this study feed on Polyporaceae, but for some of them the polypores appear to be only incidental hosts. Although some of the Oecophoridae are probably general scavengers, the tineids are for the most part obligate associates of wood-rotting Basidiomycetes. A few records are known from Ascomycetes. Schutze (1931) reported that *Nemapogon arcellus* (Fabricius) feeds in the small brown sporophores of *Hypoxylon fuscum*. During this investigation, a number of collections of *Hypoxylon thouarsianum* were processed, but the only tineids reared appeared to be incidental associates. One other species of Lepidoptera, a pyralid moth, was found to use *Hypoxylon* as a principal host (Powell, 1967). Several European species of *Nemapogon* have also become adapted to human habitats and may be found feeding in dried mushrooms, grain, dried fruit, and cork.

TECHNIQUES

In most of the earlier collections, sporophores were removed from the substrate and brought into the laboratory. At times tineids may be reared in large numbers using this system, particularly when the sporophores are large, but additional field work during the years 1964–66 has shown that moth larvae are frequently located in the bark or other woody substrate underlying the fungal fruiting body. Most of our later collections have involved caged logs, branches, or bark chunks with sporophores and sterile fungus tissue under the bark or protruding from cracks.

Wax-lined cardboard cartons to which moisture is added every few days have proved to be suitable housing for larger fungus collections. These cartons must be opened daily during periods of active emergence, because tineids do not consistently move out towards the light and into emergence vials, as do most moths. For smaller collections "Tupperware" trays with tight fitting lids proved effective in preventing moisture loss.

In addition to our own collections, we have included records from specimens bearing host labels the source of which could not be checked. Thus some of the records from older pinned specimens may not be accurate. In Table 1, a distinction is made between verified and non-verified host associations. In the sections presenting biological data, the abbreviations "emgd." (emerged) and "r.f." (reared from) are used. The number of specimens reared is not accorded special significance. In many cases, emergences of only one or a few individuals may be attributed to the conditions of collection or rearing, as explained above.

In our own collections (JFL and JAP lot numbers given in the data), representative samples of the fungi were separated and allowed to dry for identification purposes. Host determinations were provided by specialists cited in the acknowledgments. As the study progressed, we developed index collections of the fungi and identified some of the more common species ourselves.

THE HOST FUNGI

Since an attempt will be made to determine the degree of host or habitat preference exhibited by fungus-feeding moths, it will be useful to examine the nature of the fungus substrate, the classification of the host fungi, their distributional and ecological ranges, and the possible factors which might be involved in the selection

TABLE 1. SUMMARY OF HOST RECORDS FOR NORTH AMERICAN FUNGUS-FEEDING TINEIDAE

Fungus species → / Moth species	Hypoxylon thouarsianum	Armillaria mellea	Stereum hirsutum	Merulius americanus	Ganoderma applanatum	Ganoderma brownii	Ganoderma lobatum	Fomes pinicola	Fomes officinalis	Fomes igniarius	Fomes pini	Polyporus gilvus	Polyporus circinatus	Polyporus dryophilus	Polyporus vulpinus	Polyporus munzii	Polyporus amarus	Polyporus sulphureus	Polyporus adustus	Polyporus anceps	Polyporus volvatus	Polyporus versicolor	Polyporus hirsutus	Lenzites betulina	Trametes hispida	Daedalea microsticta	Poria versipora	Fungus species	Verified records
Nemapogon granellus	1					1						3	1					(2)					1					6	7
Nemapogon molybdanellus	4				1	(1)		2	1	1		9						1	2		1	1 (1)					1	12	24
Nemapogon apicisignatellus														1					2									2	3
Nemapogon oregonellus											(1)						2 (1)											2	2
Nemapogon detectellus		1												1 (1)	1	4		(1)							1 (1)			6	8
Homosetia maculatella				1									1					1										3	3
Monopis mycetophilella												1										1						2	2
Celestica sp.			1																									1	1
Morophaga cryptophori																					8 (1)							1	8
Diataga leptosceles															1											1		2	2
"Scardia" coloradella					1		1													1								3	3
"Scardia" gracilis	1		1					1				7						1	1		1	2		1				9	16
"Scardia" berkeleyella												1										1						2	2
Number of moth species	3	1	2	1	2	2	1	2	1	1	1	5	2	2	2	1	1	5	3	1	3	4	1	1	1	1	1	X	X
Number of verified records	6	1	2	1	2	1	1	3	1	1	0	21	2	2	2	4	2	3	5	1	10	5	1	1	1	1	1	X	77
Total fungus collections	24	1	22	1	12	20	1	65	7	3	4	28	2	4	2	7	2	9	22	13	52	141	19	18	13	3	5	X	497
Index of productiveness	.25	X	.09	X	.17	.05	X	.05	.14	X	X	.75	X	X	X	.57	X	.33	.23	.08	.19	.03	.05	.05	.08	X	.20	X	X

of particular fungi as feeding or oviposition sites. All of the fungus species encountered in this study cause decay in woody plants, and, with the exception of the ascomycete *Hypoxylon thouarsianum*, they are advanced members of the Basidiomycetes (families Agaricaceae, Thelephoraceae, and Polyporaceae) in which the hymenium or spore-bearing surface forms part of a relatively large and persistent fruiting body or sporophore. Often the major portion of the fruiting body consists of sterile hyphal tissue and is called the context; it is this part of the sporophore which is utilized as food by many insect species.

Classification. In recent years several attempts have been made to revise the classification of the Polyporaceae and related families, using microstructure (Cunningham, 1965) and cultural characters (Nobles, 1958, 1965), in addition to the general habitus of the fruiting body and the characteristics of the hymenium and spores. At present, however, no system has been widely accepted; numerous generic names have been proposed, and the application of a particular name varies from author to author. Because of this confusion, some authorities, such as Lowe and Gilbertson (1961a, b), have found it more convenient to use the older concepts of Fries and others until an acceptable generic classification has been developed. Cunningham (1947) points out that many of the Friesian concepts are relatively useless, and he gives as examples certain species of polypores which vary to the extent that they could be placed in any one of five genera. Labels such as "ex *Polyporus*" or "ex *Fomes*" on fungus-bred insect specimens are of little or no value in determining host relationships and are excluded from consideration here. At the species level, however, the North American polypores are fairly well known, and several current manuals are available (Lowe, 1957, 1966; Lowe and Gilbertson, 1961a, b; Overholts, 1953).

The following is a list of host fungi from which North American tineids have been reared:

ASCOMYCETES, XYLARIACEAE
- *Hypoxylon thouarsianum* (Leveille) Lloyd (= *Hypoxylon occidentale* Ellis and Everhart)

BASIDIOMYCETES, AGARICACEAE
- *Armillaria mellea* (Vahl) Quelet

BASIDIOMYCETES, THELEPHORACEAE
- *Stereum hirsutum* Willdenow ex Fries

BASIDIOMYCETES, POLYPORACEAE
- *Daedalea microsticta* Cooke
- *Fomes igniarius* (Linnaeus ex Fries) Kickx
- *Fomes officinalis* (Villars ex Fries) Faull
- *Fomes pini* (Thore ex Persoon) Lloyd
- *Fomes pinicola* (Swartz ex Fries) Cooke
- *Ganoderma applanatum* (Persoon ex Wallroth) Patouillard
- *Ganoderma brownii* (Murrill) Gilbertson
- *Ganoderma lobatum* (Schweinitz) Atkinson
- *Lenzites betulina* (Linnaeus ex Fries) Fries
- *Merulius americanus* Burt
- *Polyporus adustus* Willdenow ex Fries
- *Polyporus amarus* Hedgcock
- *Polyporus anceps* Peck
- *Polyporus circinatus* Fries
- *Polyporus dryophilus* Berkeley
- *Polyporus gilvus* (Schweinitz) Fries
- *Polyporus hirsutus* Wulfen ex Fries
- *Polyporus munzii* Lloyd
- *Polyporus sulphureus* Bulliard ex Fries
- *Polyporus versicolor* Linnaeus ex Fries
- *Polyporus volvatus* Peck
- *Polyporus vulpinus* Fries
- *Poria versipora* (Persoon) Romell
- *Trametes hispida* Baglietto

The genus *Merulius* has a doubtful place among the polypores and has been placed

in a separate family by some authorities; some species superficially resemble *Stereum* and other Thelephoraceae in having a thin context and relatively continuous hymenial surface (very shallow pores). The species of *Ganoderma* are all closely related and seem to form a natural group. The remainder of the polypores above represent a diverse assemblage, but at least three natural units can be recognized that do not correspond to the generic groupings presented here. *Fomes igniarius*, *F. pini*, and *Polyporus gilvus* have rather hard and woody, often perennial, sporophores in which the context is distinctly reddish brown or yellowish brown, turning black with the application of KOH solution; these species have been placed in the genus *Phellinus* Quelet by some authorities (Bondarzew, 1953). *Polyporus circinatus*, *P. dryophilus*, *P. vulpinus*, and *P. munzii* also have a brownish context that reacts similarly with KOH, but sporophores are annual, the texture is not as hard and woody, and older specimens tend to crumble; these species are sometimes included in the genus *Inonotus* Karsten. Nobles (1958) places both of these groups in the same section on the basis of cultural characters. *Polyporus versicolor*, *P. hirsutus*, *Lenzites betulina*, and *Trametes hispida* have a whitish or tan context with a fibrous or punky texture and a complex (trimitic) hyphal system; these and a number of other species seem to form a natural group that roughly corresponds to the genus *Coriolus* Quelet.

The fungus substrate. Two features shared by all of these fungi are: 1) their association with woody plants, and 2) the relative toughness and durability of the fruiting body. In contrast to the terrestrial members of the Agaricaceae and Boletaceae, these wood-rotting fungi usually occur off the ground on living or dead trees, logs, and stumps, and the fruiting body is less susceptible to water-logging and rapid bacterial and fungal decay. The context is often woody or fibrous, and even in the annual species the fruiting body may be persistent throughout the year. As a result, the habitat formed is suitable for a number of Lepidoptera and Coleoptera which have a relatively long life cycle but are capable of feeding within a tough and often dry substrate. In addition, the base of the sporophore is continuous with the wood, which has been chemically altered by the fungus mycelium; this permits the occasional use of the fruiting body by insects which normally occur in rotting wood or conversely provides an alternate substrate for feeding or pupation by insect inhabitants of the sporophores. As mentioned above, a number of moth larvae have been found within the wood.

Factors involved in host or habitat selection. Important in the present study are those factors common to only one or a few of the fungi which might make them suitable for or preferred by some insect species but not others. These include the structure of the fruiting body itself, the type of rot produced in the wood, the characteristics of the host trees, and the nature of the general habitat in which the fungus is normally found.

One obvious character, briefly mentioned above, is the color of the sporophore, which is a reflection of its chemical composition. Lawrence (1967) and Paviour-Smith (*in litt.*) have found that certain species of the beetle family Ciidae occur only on those fungi with brownish sporophores. The species of *Ganoderma* and the *Phellinus* and *Inonotus* groups all have brownish fruiting bodies, while in all of the other polypores listed above, the context is whitish to pale brown and does not turn black in KOH. The fruiting body of *Armillaria mellea* has a light colored context, while *Hypoxylon thouarsianum* produces a brownish sporophore, which turns black and cinder-like with age.

The texture of the fruiting body varies considerably, but it is often difficult to characterize. Paviour-Smith (1960) and Lawrence (unpublished data) have noted that a number of ciid beetles are restricted

to fungi with a trimitic hyphal system and a whitish or pale context (*Polyporus versicolor* and its relatives). It is possible, however, that the nature of the hyphal system is not directly correlated with texture, and the type or extent of extracellular adhesive material or the thickness of the hyphal walls may be as important as the presence of binding hyphae. This matter is complicated by the fact that texture (as well as chemical composition) varies with age and moisture conditions. In some species (*Fomes pinicola*, the *Phellinus* group) older specimens become hard and woody, in some (*Ganoderma*, the *Coriolus* group) they are firm but fibrous or punky, in some (*Inonotus* group) they may be more loosely fibrous, tending to break up easily, and in others (*Polyporus sulphureus* and *Fomes officinalis*) they may be chalky or friable. In his discussion of the successive changes taking place in the fruiting bodies of polypores, Graves (1960) makes a distinction between those sporophores growing in wet conditions (stage 4b) and those which have been allowed to dry out (stage 4a). In a fungus such as *Ganoderma applanatum*, there is a distinct difference between wet and dry fruiting bodies, and this is reflected in the composition of the insect fauna.

The size and thickness of the sporophore and its persistence determine the amount of food available to sustain the insect population when the wood cannot be used as an alternative substrate. Species of *Fomes* and *Ganoderma* often produce massive fruiting bodies which are often perennial, forming new layers each year; sporophores of most of the other species are annual and vary in size. In *Stereum* and *Merulius* the context is very thin, in *Polyporus adustus*, *P. gilvus*, and the *Coriolus* group it is somewhat thicker, and in *P. amarus* or *P. dryophilus* it may be quite thick. Some species, such as *P. gilvus* and *P. adustus*, have relatively small fruiting bodies, but large numbers of them often occur together connected by sheets of sterile tissue; in other species, such as *P. volvatus* and *H. thouarsianum*, they are always small and isolated from one another. Although *P. sulphureus* or *Armillaria mellea* are usually ephemeral and the woody *Fomes* usually persistent, it is difficult to determine the relative durability of most fruiting bodies because of the effects of moisture conditions, bacterial and fungal breakdown, and the damage produced by the numerous species of fungus-feeding insects.

Most species of polypores have relatively wide host ranges, but a few are host specific and most others occur primarily either on gymnosperms or angiosperms. The two types of decay produced are the white or delignifying rot and the brown or carbonizing rot. *P. amarus* occurs exclusively on *Libocedrus decurrens*, where it causes a brown rot, *P. vulpinus* and *P. munzii* produce white rot in *Populus* and *Salix*, and *G. brownii* usually grows on living or dead *Umbellularia californica*. The species occurring primarily on gymnosperms are *M. americanus*, *F. pinicola*, *F. officinalis*, *F. pini*, *P. circinatus*, *P. sulphureus* (in western North America), *P. volvatus*, and *P. anceps;* of these *F. pinicola*, *F. officinalis*, and *P. sulphureus* produce brown rots. *P. gilvus*, *P. dryophilus*, *P. versicolor*, and the rest of the species listed above occur primarily on angiosperms, and all produce white rots.

Since little work has been done on the detailed distribution or local abundance of fungus species, notes on the general habitat must be based mainly on our own observations and restricted to the more common species. *H. thouarsianum*, *S. hirsutum*, *P. dryophilus*, *P. gilvus*, *P. adustus*, and *P. versicolor* are all fairly common on *Quercus* and other hardwoods in mesic areas along the Pacific Coast and Sierran foothills; in the same areas *Ganoderma brownii* commonly occurs on *Umbellularia*. Coastal and montane coniferous forests provide the habitat for *F. pinicola*, *F. pini*, *P. amarus*, *P. volvatus* and other fungi on gymnosperms. *P. vulpinus* occurs from very

low elevations to high montane regions, but it is usually found in relatively dry situations in association with *Populus;* in contrast, its closest relative, *P. dryophilus*, occurs on *Quercus* in more mesic situations. The two most characteristic fungi encountered in the low arid parts of California and Arizona are *P. munzii* and *T. hispida*, which occur on *Populus Fremontii* and *Salix* spp. Further generalizations cannot be made because of lack of records, and those above must certainly be considered tentative.

HOST RANGES OF THE MOTHS

Almost without exception, the fungus species are more widespread than the insects that feed in them. Many of the hosts are Holarctic or even cosmopolitan in distribution and occur on a wide variety of tree species. The distributions of the moths are not determined by those of their hosts, since the Lepidoptera in most cases are neither limited to a single species of fungus nor as widespread as the fungi on which they occur. Thus both host selection and geographical distribution appear to be related to ecological factors other than food.

Among the 18 species of Lepidoptera encountered during this study, those which were reared at four or more localities provide the data for the assessment of host preference in the following discussion. Information available in the literature and on most older specimens is of little use in developing generalizations concerning host specificity. Either no specific fungus determination has been given or the moth identification can be considered suspect owing to the premature state of taxonomy at the time.

In our investigation we have considered some fungi as "incidental hosts" because the sporophores are seasonal and either decay relatively quickly or harden severely. It seems likely that the fruiting bodies of some fungi are not adequate to support populations of the moths on a continuous basis over a period of years. It is assumed that polypores with large, perennial sporophores or with typically aggregated smaller ones, connected by exposed sterile tissue, provide necessary population reservoirs from which individuals move out to establish colonies in less permanent substrates. *Hypoxylon thouarsianum*, for example, has produced moths in about 25 per cent of our collections of it. In each case, however, only one or a few adult Lepidoptera emerged, and the fungus was found growing in association with sporophores of another species occupied by tineids in greater numbers. This suggests that the small and isolated fruiting bodies of *Hypoxylon*, which become relatively hard during the dry season, cannot support permanent populations of tineid moths in the ecological situations we have observed. A comparable situation probably exists with many Thelephoraceae and Polyporaceae as well, either because the fruiting bodies are not persistent (*Polyporus sulphureus*) or because they usually offer only sparse larval habitats (*Polyporus versicolor*, *Stereum hirsutum*). Rearing records from these "incidental hosts" may mask generalizations about host range or host specificity.

It is likely that many insects normally occurring on fungi may under given conditions feed on a variety of other substances. Thus, the European *Nemapogon granellus* has been recorded feeding in various stored food products, such as grain, meal, and dried mushrooms, as well as on Polyporaceae in nature (Schutze, 1931; Hinton, 1956). The ciid beetle, *Cis bidentatus* (Olivier), has been reared on stale bread and orange rinds in the laboratory (Fletcher, 1895), although it normally feeds on *Polyporus betulinus* and certain other fungi (Paviour-Smith, 1960). Similarly, it may be expected that in the field, substrates other than the principal host fungus will occasionally serve as food material. In one such case, the sporophore of a wood-rotting agaric, *Armillaria mellea*, was found to harbor a colony of *Nemapogon defectellus*. This moth had been reared from *Trametes*

hispida at the same site on a previous occasion. It is assumed that the ephemeral nature of the *Armillaria* fruiting body eliminates any possibility of a moth population depending entirely upon this host. The same is probably true of other wood-rotting Agaricaceae, such as *Pleurotus ostreatus*, which we sampled several times without finding any evidence of Lepidoptera activity.

Criteria developed by Lawrence (1967) to evaluate possible incidental host records for Ciidae are not easily applicable to Microlepidoptera. In that study the presence of 10 or more adults or one or more immatures was taken as evidence of a breeding colony. Collections involving only a few adults were considered incidental. Using this method, *Ceracis thoracicornis* (Ziegler), for example, was found to have breeding records for only 14 of the 30 species of fungi from which it had been taken. During the present investigation the numerical density of larvae was not assessed. Adults reared indicate the presence of larvae or pupae at the time of collection, but in negative samples the possible presence of young larvae that were unable to complete their development under the rearing conditions cannot be ruled out. The actual number of individuals reared is not a consistent index of larval density owing to differences in the size of fruiting bodies, sample size, maturity of larvae at the time of collection, and the treatment of the sample after collection. Thus for the moths, consistent low numbers of individuals reared can be used only as supplementary evidence that a particular host is incidental.

Oecophoridae. In the Oecophoridae few rearings have been conducted under careful surveillance enabling recognition of the feeding substrate of even mature larvae. Nothing is known about the oviposition behavior or the feeding sites of young larvae. In general, it appears that fungus-feeding oecophorids and *Oinophila* have broader feeding ranges than fungus-feeding tineids. Some may be scavengers in abandoned insect galleries, possibly only or mainly when the debris is moldy, and the use of wood-rotting fungi as a larval habitat may be incidental. This is true for *Endrosis sarcitrella*, probably is true for *Borkhausenia fuscescens*, and may be for *B. coloradella*. The last species will feed in bark, at least in diseased spots and during the construction of pupation galleries. *Borkhausenia quadrimaculella* may have similar habits but apparently is limited to coniferous tree associations.

The four records available for *Eumeyrickia trimaculella* have involved sporophores of Polyporaceae, and this species may be found to be limited to these hosts, possibly with narrow ecological restrictions limiting the range of species used, as in the case of some tineids.

Tineidae. The Tineidae considered here, by contrast, are strictly fungus feeders in the larval stage and are associated primarily with polypores.

A discussion of host ranges in North American tineids must be prefaced by a mention of the premature state of the taxonomy of this group at the present time. For the Palaearctic region, Hinton (1955, 1956), Petersen (1957, 1958), and Zagulajev (1959, 1960, 1964) have provided a sound basis for systematic work in the Tineidae. The concepts used by these workers, however, have not previously been applied to American members of the family, and the arrangement of genera in present checklists is more or less superficial, dating back to the work of Dietz, shortly after the turn of the century.

Thus the genus *Tinea*, as listed by McDunnough (1939), included a diverse assemblage of members of two or three subfamilies of Old World authors. Both animal and plant product feeders are represented, including most of the Nearctic species that are congeneric with the European *Nemapogon*, the largest Holarctic group of fungus-feeders. A few species representing other nemapogonine genera were encountered during this study, but their generic

assignments in our treatment should be considered tentative.

A series of species treated in the American literature under the genus name *Scardia* were also reared in the course of our work. Although these are not congeneric with *Scardia polypori* of Europe, they are members of the Scardiinae. For the purposes of the present study, it seems best to leave them assigned to "*Scardia*" rather than propose a new genus for them.

At the species level there remain some unsolved problems relative to the moths treated below. These have been discussed elsewhere (Powell, 1968a). Type material of nearly all American species of Scardiinae and Nemapogoninae have been examined, but genital characters of most have not been studied. In addition, several of Chambers's species are based on specimens which may be no longer extant. The fact that most Nearctic members of both of these subfamilies were originally described from eastern states, while virtually all of our material is western, has also affected the recognition of species. As a result, two or three of the forms discussed below may eventually be found to represent undescribed species where an old name is here applied. In these cases, however, previously described, related species have no known fungus associations, so that our speculations on host ranges should not be affected by subsequent changes in nomenclature. Preparations and comparisons of genitalia have been made for representatives of all series reared; thus, conclusions on species limits within our material are accurate, even if changes in the interpretation of names are applied later.

Table 1 summarizes host association information given below in the "biological data" for 13 species of Tineidae. Numbers without parentheses represent records which we consider "verified," whether one or many moths were reared. Verified records include all our own collections (those designated with JFL or JAP lot numbers in the data), a few collections made by contemporary workers where host determinations can be considered accurate, and those from museum collections where identifiable samples of the host fungus were preserved with the moths. Numbers in parentheses represent records from the literature or from specimens that are not verified as to host identification.

An "index of productiveness" is given for each fungus species of which more than four collections were made. This represents the ratio of the number of verified records for a particular fungus to the total number of collections made of that fungus. Since more than one species of tineid may be reared from a single lot, a value greater than 1.0 is theoretically possible. A strong collecting bias was shown, especially during the early part of the study, for *Polyporus versicolor* and certain other fungi that have a greater number of ciid beetles associated with them. These collections were purposely not kept damp, and woody substrate subtending the sporophores usually was not taken. By contrast, species such as *Polyporus gilvus*, which are not productive for Ciidae in California, were not emphasized early in the study. Subsequently, they have proved to be principal hosts of tineids, and the collecting of them has increased, with more emphasis being placed on proper rearing methods for moths. Thus index values given in the table may not be entirely comparable between species, but they should serve to indicate the more consistently used fungus types. It can be seen from these index values that certain fungi, especially the related *Polyporus gilvus* (0.75) and *P. munzii* (0.57), are more frequently inhabited by tineids than are others (e.g., *Stereum hirsutum*, 0.09; *Fomes pinicola*, 0.05; or *Polyporus versicolor*, 0.03).

Among species with indices higher than the overall average of 0.19, *Hypoxylon thouarsianum* (0.25) and *Polyporus sulphureus* (0.33) have been discussed above and classified as "incidental hosts." In the case of the former, the high index is prob-

ably due to the frequent occurrence of this species in close association with *Polyporus gilvus* on dead *Quercus agrifolia. Polyporus sulphureus,* on the other hand, sometimes harbors large colonies of *Nemapogon,* and in ecological situations where sporophores are more persistent this species may constitute a principal host.

Polyporus volvatus (0.19) constitutes a special case, since it is the principal host of *Morophaga cryptophori* but probably serves as an incidental host for other tineids. Excluding records for *M. cryptophori, P. volvatus* has an index of only 0.04.

The Tineidae appear to comprise two groups with reference to their host ranges: a) host specific species, and b) ecologically restricted species, which utilize various wood-rotting fungi as they become available in the habitat. We found no species with both broad host acceptance and wide ecological tolerance, so that it occurred together with several other species. Five species of *Nemapogon* were represented in the more than 90 productive collections listed in our data, but in no case did more than two species of *Nemapogon* share the same host species in sympatry. Among the 13 species of Tineidae reared, no single collection included more than two species, although all four moths using *P. versicolor* were taken in central California Coastal Transition Zone localities and certainly could occur together. The highest number of moth species recorded for a single fungus was four (*P. sulphureus* and *H. thouarsianum,* in addition to *P. versicolor*). It is interesting that all three of these are considered to be incidental for at least two of the tineids involved.

Host specific species. The best example of apparent host specificity is that of *Morophaga cryptophori,* which has been reared at nine widely scattered California localities from *Polyporus volvatus* and was originally described from that fungus in Idaho. Most of our collections yielded only one or two adults each, but the small size of *P. volvatus* sporophores may be a causal factor in the low numerical density of larvae. About 15 per cent of our collections of *P. volvatus* were productive for this moth, while all of the other fungi, such as *Fomes pinicola,* occurring in the same conifer associations were negative for it.

A second possible host specific species is *Nemapogon oregonellus.* On three separate occasions this species has been reared from *Polyporus amarus,* a fungus which is specific to *Libocedrus decurrens.* A fourth record from *Fomes pini* on *Pseudotsuga* was a Hopkins' collection involving an appreciable series of reared adults. Presuming the identification is correct, *Fomes pini* might be an incidental or occasional host for this moth species.

Ecologically limited species. Most of the Tineidae encountered during this study fall into this category. A spectrum from narrow to rather broad ecological tolerance is shown, but no species is so catholic in occurrence that it can be expected in any wood-rotting fungus in both boreal and austral areas, for example, throughout California.

The best examples of ecological isolation are those of our two most commonly sampled species, *Nemapogon molybdanellus* and *N. defectellus.* The latter is an austral species. Two of our collections of it were made in Transition Zone localities, while 10 of the collections are from Upper Sonoran situations. The species occurs in fungi on *Salix* or *Populus* growing along stream beds in arid or semi-arid regions. *Nemapogon molybdanellus,* by contrast, has been reared at 19 localities ranging from Coastal Transition Zone to the Canadian Zone at 6000 feet in the Sierra Nevada. Although 16 fungus species are recorded for these two *Nemapogon, Polyporus sulphureus* is the only host common to both, and this fungus is probably an incidental food plant in both cases. These two moths could occur together at a dry Transition Zone site, such as the oak woodland of the Inner Coast Range in California. Both

have been collected at Mt. Diablo, Contra Costa County, in similar situations, but the two have not been found coinhabiting the same fungus. "*Scardia*" *gracilis* seems to have a range similar to that of *N. molybdanellus*, but no generalizations can be made about the remaining species treated below due to the paucity of rearing records.

On the basis of the data presented here, it appears that the majority of fungus-feeding Tineidae, at least in western North America, are polyphagous, and that only one, *Morophaga cryptophori*, is host specific. It also appears that *Polyporus gilvus* and certain related brownish fungi, such as *P. munzii*, are frequently inhabited by Tineidae, and that *P. versicolor* and its relatives are not common hosts of these moths. This may by contrasted with the situation in the beetle family Ciidae. Paviour-Smith (1960) and Lawrence (1967) have shown that ciids often prefer a certain group of related fungi, such as the *Polyporus versicolor* group (*Coriolus*) or the *P. gilvus* group (*Phellinus*). Almost every species of tineid encountered in this study was reared from fungi belonging to both groups. Moreover, *P. gilvus* and other brownish fungi, in western North America, are rarely inhabited by Ciidae, while *P. versicolor* is a common host and may harbor up to seven species in central California.

TINEIDAE

NEMAPOGONINAE

Nemapogon granellus (Linnaeus)

Tinea granella Linnaeus, 1758, Syst. Nat., ed. 10, 1: 573.
Nemapogon granellus; Petersen, 1957, Beitr. Ent., 7: 68.

This species has become adapted to a wide variety of habitats associated with man's activities, in addition to occurring on a variety of Polyporaceae. Known as a grain moth to Linnaeus, *N. granellus* has been transported with commerce to many parts of the world, and it has been recorded from such diverse situations as dried mushrooms, cork, dried fruit, and plant bulbs (Hinton, 1956).

Nemapogon granellus probably has been established on the west coast of North America for a century or more, but its occurrence there has not been documented. Our collections suggest that the species has become established in a diverse array of natural habitats in the coastal parts of California. We have not encountered the species at higher elevations in the state.

Biological data.—CALIFORNIA: ALAMEDA CO.: Berkeley, VIII-1-27, 3 ♂♂ ex mushrooms in storage (E. C. Van Dyke); same locality, V-20-51, 2 ♂♂ ex mummified peach (W. W. Middlekauff); same locality, VII-19-60, 1 ♀ r.f. *Ganoderma brownii* on *Acacia* (J. F. Lawrence, JFL 645); U. C. Campus, Berkeley, VII-30-65, 2 ♂♂, 1 ♀ r.f. *Polyporus hirsutus* on *Quercus agrifolia*, emgd. VIII-12-65 (J. Powell, JAP 65G4); Berkeley Hills nr. Claremont Cyn., II-10-67, 1 ♂, 1 ♀ r.f. *Hypoxylon occidentale* [= *H. thouarsianum*] on *Quercus agrifolia*, emgd. II-28, III-31-67 (J. Powell, JAP 67B4); same locality, II-14-67, 3 ♂♂, 1 ♀ r.f. *Quercus agrifolia* bark and log with *Hypoxylon occidentale*, emgd. III-3 to IV-9-67 (J. Powell and P. A. Rude, JAP 67B6, B7); same locality, V-2-67, 3 ♂♂, 1 ♀, flying 6:00 PM assoc. with fallen *Quercus agrifolia* and *Hypoxylon occidentale* (J. Powell); Piedmont, XII-66, 1 ♂ r.f. oleander branch with black scale, emgd. II-13-67 (K. S. Hagen). MARIN CO.: Mill Valley, IX-18-56, 1 ♂ r.f. *Lithocarpus densiflorus* log (H. B. Leech); Alpine Lake, I-19-67, 1 ♀ r.f. *Polyporus gilvus*, emgd. II-27-67 (P. A. Rude, JAP 67A10). MONTEREY CO.: Carmel, V-15-60, 1 ♂, 2 ♀♀ r.f. *Polyporus circinatus* on *Pinus radiata*, emgd. VI-10-60 (J. F. Lawrence, JFL 571). RIVERSIDE CO.: Riverside, III-4-61, ♂♂ ♀♀ r.f. *Polyporus sulphureus* on *Eucalyptus*, emgd. III-24-61 (P. H. Timberlake). SAN MATEO CO.: 1 mi. E La Honda, III-31-61, 1 ♀ r.f. *Polyporus gilvus* on *Umbellularia californica*, emgd. IV-10-61 (W. Azevedo, JFL 784); Menlo Park, XI-5-59, 1 ♂, 2 ♀♀ r.f. *Polyporus sulphureus*

(C. Duncan). SANTA BARBARA CO.: Prisoner's Harbor Creek, Santa Cruz Island, V-1-66, ♂♂♀♀ r.f. *Polyporus gilvus* on *Quercus agrifolia*, emgd. VI-15 to VIII-26-66 (J. Powell and J. Wolf, JAP 66E3).

Nemapogon molybdanellus (Dietz)

Tinea molybdanella Dietz, 1905, Trans. Amer. Ent. Soc., 31: 61.
Nemapogon molybdanellus; Powell, 1968, Pan-Pac. Ent., 43: 293.

This species, which was originally described from Pasadena, California, has been the most commonly encountered fungus moth in our survey. It is geographically and ecologically widespread in California, having been collected from sea level up to 6000 feet in the Sierra Nevada. We have reared *N. molybdanellus* from about a dozen species of Polyporaceae and Xylariaceae.

Biological data.—CALIFORNIA: ALAMEDA CO.: Berkeley, V-29-60, 1♂, 1♀ r.f. *Poria versipora* on *Umbellularia californica*, emgd. VI-16-60 (J. F. Lawrence, JFL 581); Oakland, 1♂ r.f. *Polyporus ?versicolor*, emgd. IV-15-60 (no further data); Oakland Hills (Redwood Rd.), II-9-66, 3♂♂, 2♀♀ r.f. *Hypoxylon occidentale* [= *H. thouarsianum*] on *Quercus agrifolia*, emgd. II-29 to V-11-66 (J. Wolf, JAP 66B9); same data, 1♂ r.f. *Polyporus versicolor* on *Quercus agrifolia*, emgd. IV-15-66 (J. Wolf, JAP 66B11). CONTRA COSTA CO.: Tilden Park, Berkeley Hills, IX-10-62, 1♂ r.f. *Polyporus adustus* (P. deBenedictis, JFL 1102); same locality, II-4-66, 2♀♀ r.f. *Fomes igniarius* on *Quercus agrifolia*, emgd. IV-1 to IV-15-66 (A. J. Slater and J. Wolf, JAP 66B16); Russell Property, 4 mi. NE Orinda, XII-31-66, ♂♂♀♀ r.f. *Ganoderma ?brownii* on *Quercus agrifolia*, emgd. I-26 to III-22-67, IV-3 to IV-20-67, V-1-67 (J. Powell, JAP 67A5); 6 mi. S Clayton, I-22-61, 2♂♂, 2♀♀ r.f. *Polyporus sulphureus* on *Quercus agrifolia*, emgd. II-3 to II-27-61 (J. F. Lawrence, JFL 748). MARIN CO.: Alpine Lake, VII-7-66, 3♂♂, 2♀♀ r.f. *Polyporus gilvus* on *?Lithocarpus*, emgd. VIII-18 to IX-22-66 (P. A. Rude and J. Wolf, JAP 66G4); 1 mi. S Inverness, III-17-66, 1♂ r.f. *Polyporus gilvus* on *Quercus agrifolia*, emgd. V-16-66 (J. Wolf, JAP 66C16); same data, 1♀ r.f. *Ganoderma applanatum* on *Umbellularia californica*, emgd. V-24-66 (J. Wolf, JAP 66C18). MONTEREY CO.: Big Sur, IV-16-61, 1♀ r.f. *Polyporus gilvus* on *Umbellularia californica* (J. F. Lawrence, JFL 795). SANTA BARBARA CO.: 6 mi. SE Lompoc, VII-9-65. ♂♂♀♀ r.f. *Polyporus gilvus* on *Quercus agrifolia*, emgd. VIII-10 to VIII-30-65 (J. Powell, JAP 65G3); same locality, I-17-66, ♂♂♀♀ r.f. *Polyporus gilvus* on *Quercus agrifolia*, emgd. II-11 to III-22-66 (J. Powell, JAP 66A17, A18); same data, 1♂ r.f. *Hypoxylon occidentale* on *Quercus agrifolia*, emgd. II-17-66 (J. Powell, JAP 66A22); same locality, IV-23-66, 1♂, 1♀ r.f. *Polyporus gilvus* on *Quercus agrifolia*, emgd. IV-24-66 (J. Powell, JAP 66D24); Prisoner's Harbor Creek, Santa Cruz Island, V-1-66, 5♂♂, 5♀♀ r.f. *Polyporus gilvus* on *Quercus agrifolia*, emgd. VI-15 to VIII-26-66 (J. Powell and J. Wolf, JAP 66E3); same data, 2♀♀ r.f. *Hypoxylon occidentale* on *Quercus agrifolia*, emgd. VII-13-66 (J. Wolf, JAP 66E5); Prisoner's Harbor, Santa Cruz Is., V-1-66, 1♂ r.f. *Hypoxylon occidentale* on *Quercus agrifolia*, emgd. VII-13-66 (J. Powell, A. J. Slater, J. Wolf, JAP 66E4); same data, 4♂♂, 2♀♀ r.f. *Polyporus gilvus* on *Quercus agrifolia*, emgd. V-5-66, VI-16 to VII-26-66 (J. Powell, A. J. Slater, J. Wolf, JAP 66E8). SONOMA CO.: 2.5 mi. S Cazadero, II-25-66, ♂♂♀♀ r.f. *Polyporus gilvus* on *Alnus*, emgd. III-25 to V-11-66, VIII-26, IX-9-66 (A. J. Slater and J. Wolf, JAP 66B41); Mark West Creek, 12 mi. NW St. Helena, II-18-66, 1♂, 2♀♀ r.f. *Polyporus adustus* on *Alnus*, emgd. III-25 to V-6-66 (A. J. Slater and J. Wolf, JAP 66B28); 2 mi. NW Cloverdale, VII-2-66, 1♂ r.f. *Polyporus volvatus* on *Pinus*, emgd. VII-26-66 (P. A. Rude, JAP 66G1). TEHAMA CO.: 9 mi. N Mineral, V-20-66, ♂♂♀♀ r.f. *Fomes officinalis* on *Abies magnifica*, emgd. VI-8 to IX-22-66 (J. Powell, A. J. Slater, J. Wolf, JAP 66E19).

TUOLUMNE CO.: Crane Flat, VI-16-61, 1 ♀ r.f. *Fomes pinicola* on *Abies concolor* (J. F. Lawrence, JFL 832); Dardanelle, VI-13-62, 2 ♂♂, 1 ♀ r.f. *Fomes pinicola* on *Abies* (J. F. Lawrence, JFL 1009).

Nemapogon apicisignatellus (Dietz)

Tinea apicisignatella Dietz, 1905, Trans. Amer. Ent. Soc., 31: 65.

Nemapogon apicisignatellus; Powell, 1968, Pan-Pac. Ent., 43: 295.

The three collections of this species made during our study are from Polyporaceae occurring in similar Transition Zone situations. However, the species was originally described from Pennsylvania, and if our identification is correct (Powell, 1968a), *N. apicisignatellus* probably occupies more diverse habitats in other parts of its range.

The Canadian National Collection has specimens which appear to be this species, reared from *Ganoderma applanatum*, from Bell's Corners, Ontario, V-30-59 (E. C. Becker).

Biological data.—OREGON: DOUGLAS CO.: 10 mi. SW Camas Valley, X-24-62, ♂♂♀♀ r.f. *Polyporus adustus* on *Alnus*, emgd. XI-19-28-62 (J. F. Lawrence, JFL 1126). LANE CO.: Eugene, XII-25-61, ♂♂♀♀ r.f. *Polyporus dryophilus* on *Quercus*, emgd. I-27 to II-2-62 (D. H. Janzen, JFL 986). CALIFORNIA: SANTA CRUZ CO.: 5 mi. N Felton, V-29-66, ♂♂♀♀ r.f. *Polyporus adustus* on *Quercus agrifolia*, emgd. VII-6 to IX-22-66 (A. J. Slater, JAP 66E26).

Nemapogon oregonellus (Busck)

Tinea oregonella Busck, 1900, Jour. N. Y. Ent. Soc., 8: 246.

Nemapogon oregonellus; Powell, 1968, Pan-Pac. Ent., 43: 295.

The four records available for *N. oregonellus* are of fungi associated with Douglas fir and incense cedar. Essig (1926) reported that this species breeds in woody *Polyporus* "on redwood and other coniferous trees."

Biological data.—OREGON: County unknown, nr. Parker's Station, XI-17-1914, ♂♂♀♀ r.f. *Trametes* [= *Fomes*] *pini* on *Pseudotsuga taxifolia* (P. D. Sergent, Hopk. U. S. 13206a). CALIFORNIA: MADERA CO.: Yosemite Nat'l. Park, V-34, ♂♂♀♀ r.f. *Polyporus amarus* on *Libocedrus decurrens* [host preserved with moths] (W. H. Lange, Jr.). SAN FRANCISCO CO.: San Francisco, V-7-1914, ♂♂♀♀ r.f. sporophore *Polyporus amarus* on *Libocedrus decurrens* (T. D. Woodbury, Hopk. U. S. 12176). TEHAMA CO.: Round Valley, IX-1-61, 5 ♂♂ r.f. *Polyporus amarus* on *L. decurrens* (H. B. Leech, JFL 952).

Nemapogon defectellus (Zeller)

Tinea defectella Zeller, 1873, Verhandl. Zool.-Bot. Ges. Wien, 23: 220.

Nemapogon defectellus; Powell, 1968, Pan-Pac. Ent., 43: 295.

This species was first described from San Francisco, California, and is now known to be widespread in semi-arid regions of the Southwest. Our records generally corroborate information available in the literature concerning its biology. Essig (1926) reported that *N. defectellus* breeds in woody *Polyporus* growing on cottonwood trees in New Mexico, Arizona, and California; and Linsley and Usinger (1936) encountered larvae in *Polyporus rheades* [= *P. dryophilus*] at Mt. Diablo in central coastal California. Bailey (1935) attributed the scarcity of sporophores of *P. rheades* at Mt. Diablo to the effects of insects, especially *N. defectellus*. Bailey mentioned that the larvae of this species persist even after the sporophores are extremely dry.

This is the only species of *Nemapogon* which has produced an appreciable number of individuals of a second generation from dry fungus material in the laboratory during our study. Whereas other species appear to be severely affected by drying of the substrate, and emergence of adults normally takes place only during the first few days or weeks, *N. defectellus* has continued to emerge over a four to eight month period in at least three of our collections. This represents at least one sub-

sequent generation resulting from the original emerging adults. Evidently the species has become adapted to living in arid regions in fungus substrates that are intermittently dry and available only in a desiccated condition.

N. defectellus is the most austral of the *Nemapogon* species encountered during our investigation, occurring in Transition and both Upper and Lower Sonoran Zone stations. The species seems to be especially adapted to riparian situations in arid areas, occurring on Polyporaceae associated with *Salix* and *Populus*.

Biological data.—OREGON: County unknown, Mistletoe, III-27-1915, ♂♂♀♀ r.f. "fungus fruiting body on black oak" (J. M. Miller and P. D. Sergent, Hopk. U. S. 12194). CALIFORNIA: CONTRA COSTA CO.: Mt. Diablo, I-23-34, ♂♂♀♀ r.f. *Polyporus rheades* [= *P. dryophilus*] (H. Bailey). RIVERSIDE CO.: Riverside, III-4-61, ♂♂♀♀ r.f. *Polyporus sulphureus* on *Eucalyptus*, emgd. III-24-61 (P. H. Timberlake); 4 mi. E Blythe, I-26-64, 2♂♂ r.f. *Trametes hispida* on *Populus fremontii*, emgd. II-26-64 (J. F. Lawrence, JFL 1255). SAN DIEGO CO.: Mission Dam, I-16-66, ♂♂♀♀ r.f. *Trametes ?hispida* on *Salix*, emgd. II-8 to III-18-66 (J. Powell, JAP 66A12, A13); same locality, VI-24-66, ♂♂♀♀ r.f. *Armillaria mellea* sporophore on *Salix*, emgd. VI-25-30-66, ♂♂♀♀ emgd. VIII-23 to X-27-66, 1♂ emgd. XII-5-66 (J. Powell, JAP 66F12), same data, 2♂♂, 1♀ r.f. *Trametes?* on *Salix*, emgd. VII-20, 29, IX-9-66 (J. Powell, JAP 66F11). ARIZONA: MARICOPA CO.: 5 mi. SE Wickenburg, I-26-64, ♂♂♀♀ r.f. *Polyporus munzii* on *Salix*, emgd. II-26 to VII-64 (J. F. Lawrence, JFL 1257). PIMA CO.: Sabino Cyn., Santa Catalina Mts., I-27-64, 3♂♂, 1♀ r.f. *Polyporus munzii* on *Salix* (J. F. Lawrence, JFL 1260). SANTA CRUZ CO.: Patagonia, VIII-10-61, 1♂ r.f. *Polyporus munzii* on *Populus fremontii* (J. F. Lawrence, JFL 930); 4 mi. NE Patagonia, I-29-64, ♂♂♀♀ r.f. *Polyporus vulpinus* on *P. fremontii*, emgd. V-VI-64 (J. F. Lawrence, JFL 1280); 2 mi. SW Patagonia, XI-14-64, ♂♂♀♀ r.f. *Polyporus munzii* on *Populus*, emgd. I-5 to V-3-65 (C. W. O'Brien, JAP 65A1). NEW MEXICO: CATRON CO.: 9 mi. S Luna, VII-31-61, ♂♂♀♀ r.f. *Polyporus dryophilus* on *Quercus* (J. F. Lawrence, JFL 874). TEXAS: BROWN CO.: Brownwood, XI-1-1919, ♂♂♀♀ r.f. "bracket fungus on mesquite" (no further data).

Homosetia maculatella Dietz

Homosetia maculatella Dietz, 1905, Trans. Amer. Ent. Soc., 31: 84; Powell, 1968, Pan-Pac. Ent., 43: 297.

As indicated elsewhere (Powell, 1968a), the status of this species is uncertain because a cotype of *H. maculatella* from Placer County, California, may not be conspecific with the worn type from Pennsylvania. Moreover, since the California moth lacks conspicuous upraised scale rows of the forewing, it may not be congeneric with other members of *Homosetia*.

Populations here referred to *H. maculatella* occupy an extremely diverse ecological range, from Upper Sonoran Zone in the Central Valley to timberline at 10,000 feet in the central Sierra Nevada. Apparently a wide range of fungus substrates is used, probably even moldy debris associated with decaying wood.

Biological data.—CALIFORNIA: ALAMEDA CO.: Hayward, X-28-54, 2♂♂, 2♀♀ "from fungi on damp and decaying wood" (E. G. Linsley). CONTRA COSTA CO.: 6 mi. SE Clayton, I-22-61, 5♂♂, 3♀♀ r.f. *Polyporus sulphureus* on *Quercus agrifolia*, emgd. II-17-21-61 (J. F. Lawrence, JFL 748). EL DORADO CO.: Blodgett Forest nr. Georgetown, VI-28-65, 1♂ r.f. 2 year old *Pinus jeffreyi* logs with moldy weevil galleries (I. Otvos and J. H. Borden, JAP 65H3). MONO CO.: Saddlebag Lake, 10,500 ft., VII-7-62, 1♂ r.f. *Serpula americana* [= *Merulius americanus*] on *Pinus murrayana* (J. F. Lawrence, JFL 1051). MONTEREY CO.: Carmel, V-15-60, 1♂ r.f. *Polyporus circinatus* on *Pinus radiata* (J. F. Lawrence, JFL 571). SACRA-

MENTO CO.: Sacramento, I-10-31, ♂♂ r.f. "*Poria* sp.", emgd. II-23 to III-5-31 (A. C. Browne, #3121).

TINEINAE

Monopis mycetophilella Powell

Monopis mycetophilella Powell, 1968, Pan-Pac. Ent., 43: 298.

Although a general biological characteristic of members of the subfamily Tineinae and of *Monopis* is the use of animal products as larval food, this species evidently normally feeds in fungus and associated decaying wood. Our specimens were obtained from polypores with relatively little decaying wood substrate attached. According to Forbes (1923), the larva of a closely related species, *M. croceoverticella* (Chambers), is a case bearer which lives externally on the white bracket fungus on beech. A Palearctic species, *M. fenestratella* (Heyden), has been reared from decaying wood and old, crumbling *Daedalea quercina* (Polyporaceae) (Meyrick, 1895; Schutze, 1931).

The fungi from which we have reared *M. mycetophilella* are two of our more commonly sampled species, indicating that this moth probably is non-specific in host selection. Its scarcity may in part be due to a single generation, late flight period, similar to that of *Borkhausenia coloradella*. Most of our Pacific Coast fungus collections have been made during or shortly following the rainy season.

Biological data.—CALIFORNIA: ALAMEDA CO.: Oakland, VII-1-60, 1 ♂ r.f. *Polyporus versicolor* on *Quercus agrifolia*, emgd. VII-10-60 (M. Lundgren, JFL 635). CONTRA COSTA CO.: 2 mi. SE Canyon, II-5-67, 2 ♂♂ r.f. *Polyporus gilvus* on *Quercus agrifolia*, emgd. V-1, 11-67 (J. Powell, JAP 67B1).

MEESSIINAE

Celestica species

As discussed previously (Powell, 1968a), a single specimen was reared during our survey that appears to be a species of this genus. Members of this subfamily feed on lichens, so far as is known, occurring on rock walls and in similar situations in Europe (Schutze, 1931). No species of the Nearctic fauna have as yet been referred to the series of genera treated as Meessiinae by Old World authors. However, some members of this group undoubtedly do occur in North America.

Our *Celestica* was reared from bark of *Quercus* with *Stereum* (Thelephoraceae), which was not noted to have any lichen, but may have included some.

Biological data.—CALIFORNIA: SANTA BARBARA CO.: Prisoner's Harbor, Santa Cruz Island, V-1-66, 1 ♂ r.f. *Stereum hirsutum* on *Quercus agrifolia*, emgd. V-27-66 (J. Powell and J. Wolf, JAP 66E6).

SCARDIINAE

Morophaga cryptophori Clarke

Morophaga cryptophori Clarke, 1940, Bull. So. Calif. Acad. Sci., 39: 114.

This species was described from material reared in Idaho from *Cryptophorus* [= *Polyporus*] *volvatus*. During the present study the species has been obtained from the same host, associated with *Abies* and *Pinus*, at several widely scattered stations in California.

It appears that *M. cryptophori* is a host specific feeder on *P. volvatus* and is widespread in montane areas of western North America. In Europe, *M. morella* (Duponchel), the only other member of the genus, feeds on fungus associated with nonconiferous plants, including mulberry and *Ephedra* (Dumont, 1930; Petersen, 1957c).

Biological data.—CALIFORNIA: EL DORADO CO.: N of Robb's Peak, 6000 ft., VII-1-67, 5 ♂♂ r.f. *Polyporus volvatus* on *Abies*, emgd. VII-26, 27, VIII-67 (J. Powell and R. Stultz, JAP 67G1, 3); Blodgett Forest, 13 mi. E Georgetown, VII-9-67, ♂♂ ♀♀ r.f. *P. volvatus*, emgd. VII-(23-27)-67 (W. J. Turner, JAP 67G5). GLENN CO.: Plaskett Meadows, VII-31-65, 1 ♀ r.f. *Polyporus volvatus*, emgd. VIII-27-65 (J. T. Doyen).

PLACER CO.: Squaw Valley, VIII-17-60, 1 ♂ r.f. *Polyporus volvatus* on *Pinus*, emgd. VIII-24-60 (P. deBenedictis, JFL 661). RIVERSIDE CO.: Idyllwild, VI-21-62, 1 ♀ r.f. *Polyporus volvatus* on *Pinus*, emgd. VII-10-62 (J. F. Lawrence, JFL 1022); Humber Park, 2 mi. NE Idyllwild, VI-21-62, 1 ♀ r.f. *Polyporus volvatus* on *Abies* (J. F. Lawrence, JFL 1025). SIERRA CO.: Yuba Pass, VII-7-66, 7 ♂ ♂, 3 ♀ ♀ r.f. *Polyporus ?volvatus* (W. J. Turner). TRINITY CO.: Scott Mtn. Summit, 5300 ft., 19 airline mi. N Trinity Center, VII-5-63, 1 ♀ r.f. *Polyporus volvatus* (C. D. MacNeill and V. Whitehead). TUOLUMNE CO.: Tuolumne Grove, VII-21-61, 1 ♀ r.f. *Polyporus volvatus* on *Abies concolor* (W. E. Ferguson, JFL 852).

Diataga leptosceles Walsingham

Diataga leptosceles Walsingham, 1914, Biol. Centrali-Amer., Lep. Het., 4: 375.

This species was described from Jalapa, Veracruz, Mexico, and it may be that not all of our material is conspecific. We have only two females representing a record for the species in Arizona and have not had typical material for comparison of other than external features.

The tentative identification and our fragmentary rearing information do not enable conclusions on host selection of the species. Specimens identified as *D. leptosceles* in the U. S. National Museum, collected in Trinidad, were reared from a species of "*Polyporus*."

Biological data.—ARIZONA: COCHISE CO.: 15 mi. E Douglas, VIII-5-61, 2 ♀ ♀ r.f. *Polyporus vulpinus* on *Populus fremontii* (J. F. Lawrence, JFL 908). MEXICO: VERACRUZ: Fortin de las Flores, XII-24-63, 2 ♀ ♀ r.f. *Daedalea microsticta* (C. A. Toschi and M. J. Tauber, JFL 1254).

Scardia polypori (Esper)

As discussed elsewhere (Powell, 1968a), most of the North American species currently assigned to *Scardia* probably are not congeneric with the European type of the genus, *S. polypori*. Larval characteristics of one species indicate that they are Scardiinae, but the species reared during our investigation are not referable to any Palearctic genus. They are provisionally retained as "*Scardia*" until taxonomic assessment of the North American fauna is possible.

Several Polyporaceae have been reported as hosts of *S. polypori*: *Polyporus sulphurella* [= *P. sulphureus*] and dead wood attacked by fungi in England (Hinton, 1956), *Polyporus* [= *Fomes*] *fomentarius* in Germany (Mitterberger 1910, 1911), and *Trametes gibbosa* and *Polyporus adustus* in Switzerland (Rehfous, 1955b).

"*Scardia*" *coloradella* Dietz

Scardia coloradella Dietz, 1905, Trans. Amer. Ent. Soc., 31: 25.

"*Scardia*" *coloradella*; Powell, 1968, Pan-Pac. Ent., 43: 302.

The identity of the moths we are treating under this name has been discussed previously (Powell, 1968a). Host specificity is not shown by populations of "S." *coloradella*, if colonies represented by our samples are conspecific. The general habitat is high elevation coniferous forests in each case.

Biological data.—COLORADO: EL PASO CO.: North Cheyenne Cyn., XII-11-1914, ♂ ♂ ♀ ♀ r.f. fungus at base of dead *Pseudotsuga taxifolia* (A. B. Champlain, Hopk. U. S. 12173b). ARIZONA: COCHISE CO.: Rustler Park, 8 mi. W Portal, Chiricahua Mts., VII-3-61, 1 ♀ r.f. *Polyporus anceps* on *Pinus* (J. F. Lawrence, JFL 889). UTAH: UTAH CO.: N of Mt. Timpanogos, 7300 ft., VII-30-67, 3 ♀ ♀ r.f. *Ganoderma applanatum* on *Populus tremuloides*, emgd. VIII-4 to X-67 (J. Powell, JAP 67G6). MEXICO: DURANGO: 10 mi. W El Salto, 9,000 ft., VII-23-64, 3 ♀ ♀ r.f. *Ganoderma lobatum* on *Quercus omissa*, emgd. IX-8, 9-64 and later (J. Powell, JAP 64G10, JFL 1313).

"*Scardia*" *gracilis* Walsingham

Scardia gracilis Walsingham, 1907, Proc. U. S. Nat'l. Mus., 33: 225.

"*Scardia*" *gracilis;* Powell, 1968, Pan-Pac. Ent., 43: 302.

This species exhibits a great deal of variation in external appearance and size, in part related to the condition of the substrate in which the larvae have fed (Powell, 1968a). "*Scardia*" *gracilis* was the most common member of the subfamily encountered during our survey, limited primarily to Polyporaceae with relatively large and persistent sporophores, or large colonies with extensive sterile tissue in species with small sporophores. The larvae frequently live within the decaying wood subtending the sporophores, and at times the emergence galleries occur several centimeters from the sporophores.

"*Scardia*" *gracilis* apparently has the same ecological range and host acceptance as *Nemapogon molybdanellus*, but in California *gracilis* may be limited to the Coast Range. Fungus collections from the Sierra Nevada have yielded only a single specimen of "*Scardia*," that from Buck's Lake, Plumas County. Although its genitalia are not distinguishable from other *gracilis*, this individual may not be conspecific. It is paler with more reduced dark markings than any other "*Scardia*" reared, but it is in worn condition.

Biological data.—CALIFORNIA: GLENN CO.: Plaskett Meadows, 6,200 ft., VII-3-60, 1 ♀ as adult on *Fomes pinicola* on *Abies concolor* (J. Powell, JFL 631). MARIN CO.: Alpine Lake, III-30-66, ♂ ♂ ♀ ♀ r.f. *Polyporus gilvus* on old *Lithocarpus?*, emgd. IV-11 to V-17-66 (J. Powell, JAP 66C27); same data, VII-7-66, 1 ♂ emgd. IX-22-66 (P. A. Rude and J. Wolf, JAP 66G4); same data, 1 ♀ r.f. *Lenzites betulina* on *Umbellularia*, emgd. IX-16-66 (Rude and Wolf, JAP 66G5); same locality, I-19-67, 3 ♂ ♂, 3 ♀ ♀ r.f. *Polyporus gilvus*, emgd. II-27 to IV-3-67 (P. A. Rude, JAP 67A10); 1 mi. S Inverness, III-17-66, ♂ ♂ ♀ ♀ r.f. *Polyporus gilvus* on *Quercus agrifolia*, emgd. IV-4 to VI-15-66, 1 ♂ emgd. VIII-16-66 (J. Wolf, JAP 66C16); same data, 1 ♂ r.f. *Hypoxylon occidentale* [= *H. thouarsianum*] on *Umbellularia*, emgd. III-22-66 (J. Wolf, JAP 66C17); same data, 3 ♂ ♂ r.f. *Polyporus versicolor* on *Quercus agrifolia*, emgd. IV-19 to V-11-66, 1 ♀ emgd. IX-16-66 (J. Wolf, JAP 66C18); same locality, VII-7-66, 1 ♀ r.f. *Stereum hirsutum* on *Umbellularia*, emgd. IX-16-66 (P. A. Rude and J. Wolf, JAP 66G8). PLUMAS CO.: Buck's Lake, VII-26-64, 1 ♂ r.f. *Polyporus sulphureus* (J. T. Doyen). SAN FRANCISCO CO.: Sutro Forest, San Francisco, II-20-1913, 1 ♂ r.f. *Polyporus volvatus* [host pinned with moth], emgd. IV-1-1913 (J. C. H. [uegenin]). SAN MATEO CO.: Lake Merced, III-26-1908, 1 ♂ r.f. rotten *Lupinus arboreus* stem (F. X. Williams); Mindego Creek Cyn., 1 mi. E La Honda, III-31-61, ♂ ♂ ♀ ♀ r.f. *Polyporus gilvus* on *Umbellularia*, emgd. IV-(6-19)-61 (W. Azevedo, JFL 784). SANTA CLARA CO.: 2 mi. SW Los Gatos, V-6-61, 1 ♂ r.f. *Polyporus gilvus*, emgd. V-30-61 (W. E. Ferguson, JFL 805). SANTA CRUZ CO.: 5 mi. N Felton, V-29-66, 4 ♀ ♀ r.f. *Polyporus adustus* on *Quercus agrifolia*, emgd. VIII-2-18-66 (A. J. Slater, JAP 66E26). SONOMA CO.: 1 mi. S Cazadero, II-24-63, 1 ♂, 3 ♀ ♀ r.f. *Polyporus versicolor* on *Umbellularia*, emgd. IV-14-28-63 (J. Powell, JAP 63B5, B6); 2.5 mi. S Cazadero, II-25-66, ♂ ♂ ♀ ♀ r.f. *Polyporus gilvus* on *Alnus*, emgd. III-28 to V-17-66, 2 ♂ ♂, 1 ♀ emgd. V-27 to VI-6-66, ♂ ♂ ♀ ♀ emgd. VIII-12 to IX-16-66 (A. J. Slater and J. Wolf, JAP 66B41).

"Scardia" berkeleyella Powell

"*Scardia*" *berkeleyella* Powell, 1968, Pan-Pac. Ent., 43: 303.

Although this moth, which is much smaller than other members of the genus, was discovered only recently, it appears to have a broad host range comparable to that of "S." *gracilis*. Probably it feeds in Polyporaceae of appropriate size and in associated decaying wood, but has restricted colonies owing to other factors. All collections which have been productive for this species have been made early in the year, prior to the end of the rainy season.

Biological data.—CALIFORNIA: ALAMEDA CO.: Strawberry Cyn., Berkeley Hills, I-10-63, 1 ♂ r.f. *Polyporus versicolor* on old *Quercus agrifolia*, emgd. III-8-63 (J. Powell, JAP 63A8). CONTRA COSTA CO.: 2 mi. SE Canyon, II-5-67, 3 ♂ ♂, 2 ♀ ♀ r.f. *Polyporus gilvus* on *Q. agrifolia*, emgd. III-31 to IV-9-67 (J. Powell, JAP 67B1). MARIN CO.: Hilltops S of Marin City, III-25-57, 1 ♀ r.f. dead stems *Lupinus propinquus*, emgd. IV-25-57 (H. B. Leech); Mill Valley, II-12-64, 1 ♂ r.f. log *Lithocarpus densiflorus*, emgd. IV-16-64 (H. B. Leech).

OECOPHORIDAE

Borkhausenia (Borkhausenia) fuscescens (Haworth)

Recurvaria fuscescens Haworth, 1829, Lepid. Brit., 4: 555.
Borkhausenia fuscescens; Staudinger and Rebel, 1901, Cat. Lepid. Palaear., 2: 177.

As discussed elsewhere (Powell, 1964b), this Palearctic species has been introduced into urban areas of California, and European reports relating to its biology indicate that it is a scavenger. Most of the reports are old and are vague to the extent that the larval food is not given. The habits are equally poorly known in California. Armitage (1952) suggested that *B. fuscescens* may feed in "mouldy trash or leaves," and our isolated reared specimens may have been associated with galleries of other insects or with other debris in the fungus substrates.

Biological data.—CALIFORNIA: CONTRA COSTA CO.: Tilden Park, Berkeley Hills, IX-10-62, 1 ♀ r.f. *Polyporus adustus* (P. de Benedictis, JFL 1102); Tilden Park, II-14-66, 1 ♀ r.f. *Fomes igniarius* on *Quercus agrifolia*, emgd. III-25-66 (A. J. Slater and J. Wolf, JAP 66B16).

Borkhausenia (Decantha) boreasella (Chambers)

Oecophora boreasella Chambers, 1873, Canad. Ent., 5: 189.
Decantha boreasella; Clarke, 1941, Proc. U. S. Natl. Mus., 90: 242 (synonymy).

This species is widespread over much of boreal North America and occurs in the mountains along the length of California. The record given below is the first we have seen from any locality which is other than a conifer association. Clarke (1941) stated there were no known host records. Larvae of the closely related *B. borkhausenii* (Zeller) live under loose bark of old pine trees in Europe (Schutze, 1931).

In our collection, a moth emerged from bulk material including sporophores of *Hypoxylon* on branch sections of oak, and the feeding site is unknown.

Biological data.—CALIFORNIA: SANTA BARBARA CO.: Santa Cruz Island, Prisoner's Harbor, V-1-66, 1 ♀ r.f. *Hypoxylon occidentale* [= *H. thouarsianum*] on *Quercus agrifolia*, emgd. VI-15-66 (J. Powell, A. Slater, J. Wolf, JAP 66E4).

Borkhausenia (Schiffermuelleria) quadrimaculella (Chambers)

Oecophora quadrimaculella Chambers, 1877, Cincinnati Quart. Jour. Sci., 2: 292.
Borkhausenia quadrimaculella; Kearfott, 1903, *in*: Smith, Checklist Lepid. Bor. Amer.: 115.
Epicallima quadrimaculella; Busck, 1908, Proc. U. S. Natl. Mus., 35: 202.
Schiffermuelleria quadrimaculella; Meyrick, 1922, Gen. Insectorum, 180: 27; Clarke, 1941, Proc. U. S. Natl. Mus., 90: 248 (synonymy).
Oecophora dimidiella Walsingham, 1888, Insect Life, 1: 148.

This distinctive species, which has blackish forewings marked with yellow spots, is widespread in boreal and transition zone areas of western North America. It was reported from Alberta and British Columbia, southward to Colorado and southern California by Clarke (1941), and we have seen it from the Sierra San Pedro Martir in Baja California, some 200 miles south of the international border.

Records given by Clarke indicate an association with coniferous forest trees, and we have encountered the species on several occasions in similar situations. Most collections reveal only circumstantial evidence of a fungus feeding habit, but it appears that

conifer wood-rot fungi serve as a larval habitat at least part of the time. Clarke (1941) suggested that the larvae may feed on refuse that collects in cracks in the bark, and it may be that S. *quadrimaculella* is often a scavenger in association with decaying coniferous trees.

The adults are found under bark of fallen trees and occasionally on fungus sporophores. Our collection from Blodgett Forest, listed below, consisted of several logs which had been heavily scored by weevil larvae in the cambium area. Examination of the bark after emergence of numerous *Schiffermuelleria* revealed that lepidopterous webbing and frass was associated with a variety of sites, in external cracks in the bark, in beetle galleries under the bark, and in the thick bark itself. The only cocoons with oecophorid pupal shells and larval exuviae occurred in the bark, above the level of the mouldy weevil burrows, either in flat chambers which had evidently been excavated by the moth larvae, or in one instance in the abandoned emergence trackway of a beetle gallery.

Biological data.—CALIFORNIA: CALAVERAS CO.: Bailey Ridge, 16 mi. E West Point, V-26-64, 2 ♂ ♂ r.f. *Pinus ponderosa* with *Polyporus volvatus* (G. Lanier). EL DORADO CO.: Blodgett Forest nr. Georgetown, ♂ ♂ ♀ ♀ r.f. 2 year old *Pinus ponderosa* logs killed by weevils, emgd. VI-28-64 (I. Otvos, J. H. Borden, JAP 65H3). KERN CO.: 4 mi. N Alta Sierra, IV-28-64, 2 ♂ ♂, 1 ♀ r.f. [sporophores] *Polyporus volvatus*, emgd. V-22-64 (J. Doyen). NEVADA CO.: Boca, VI-17-64, 1 ♂ under bark fallen tree (D. F. Veirs). TULARE CO.: Portugese Pass, 7 mi. SE Pine Flat, VII-5-62, 1 ♀ as adult on *Fomes pinicola* (J. Lawrence, JFL 1097). VENTURA CO.: 10 mi. NW Lake of the Woods [Mt. Pinos, 6000 ft.] VI-7-64, 1 ♂, 1 ♀ under bark *Pinus* (W. J. Turner).

Borkhausenia (Schiffermuelleria) coloradella (Walsingham), New Combination

Oecophora coloradella Walsingham, 1888, Insect Life, 1: 150.
Epicallima coloradella; Busck, 1908, Proc. U. S. Natl. Mus., 35: 201.
Ethmia coloradella; Clarke, 1941, Proc. U. S. Natl. Mus., 90: 247.

This and the following species, *Eumeyrickia trimaculella,* were referred to the Ethmiidae by Clarke (1941), primarily on the basis of a "segmented" valva in the male genitalia. Although the Ethmiidae remains a somewhat heterogeneous assemblage, not well separated from the Oecophoridae, placement of *coloradella* and *trimaculella* with the oecophorids appears to be a more realistic indication of their relationships, particularly in view of the larval habits. *B. coloradella* feeds in fungus, in dead tissue associated with diseased areas on living trees, under bark of fallen trees, or possibly on debris in galleries of other insects in these habitats. Some members of *Schiffermuelleria* and other subgenera of *Borkhausenia* are known to feed in decaying wood or fungus under bark in the Old World (e.g., Meyrick, 1895; Schutze, 1931; Jacobs, 1950), while available information indicates that all *Ethmia* are external feeders on leaves or flowers.

On the basis of extensive revisionary work (in preparation) on the ethmiids of the Palearctic by Klaus Sattler and of the New World by Powell, structural characters of the adults of the two present species indicate that they should be placed back in the Oecophoridae. Whether the subgenus *Schiffermuelleria* is sufficiently diverse to accommodate *coloradella* may have to be answered by a re-examination of *Borkhausenia*, but characters of both male and female *coloradella* are unlike their homologues in *Ethmia*, *Pseudethmia*, and *Pyramidobela*. The divided valva does not appear to be comparable to that of *Ethmia*, while a division of this type does occur in certain *Borkhausenia* (i.e., *unitella* Hübner and *incongruella* Zeller). The heavily sclerotized, ventrally curved uncus and the elongate vinculum are features *coloradella* shares with members of various subgenera of *Borkhausenia* and with no

ethmiid. The strongly curved aedoeagus, perhaps the single most universal characteristic of male Ethmiidae, is not developed in *coloradella* or in oecophorids generally. The elongate, extensible ovipositor and correspondingly elongate apophyses are traits of female *coloradella* exhibiting similarity to those shown in *Schiffermuelleria* and *Fabiola*, but differing from their counterparts in Ethmiidae. Moreover, no ethmiid bears superficial resemblance to *coloradella*, but several oecophorids have similar facies in wing shape and color, broad hindwing fringe, elongate abdomen, etc. (e.g., *Esperia sulphurella* (F.), *Borkhausenia stipella* (L.), *B. quadrimaculella* (Chamb.)).

As mentioned by Yothers (1942), the cocoon of *B. coloradella* is extremely flimsy, as in related oecophorids such as *Esperia sulphurella*. Cocoons of *Ethmia*, even multivoltine species, are dense (Powell, 1968b). Finally, the highly characteristic "anal legs" of the pupa, a feature which is well developed in all *Ethmia* so far as is known, are not present on the pupa of *B. coloradella*. Its caudal structures are similar to those of *E. sulphurella* and *B. quadrimaculella*, both of which possess a single, stout, terminal rod which is directed posteriorly.

Borkhausenia coloradella is widespread in boreal parts of North America, from Ontario and New York to British Columbia and the northwestern United States, southward to northern Arizona and central California. Rearing records suggest a biology for *B. coloradella* similar to that of *B.* (*Schiffermuelleria*) *quadrimaculella*, discussed above. The present species often emerges from caged logs or in similar forestry practice situations and has been reared from fungus sporophores during our study. In addition, D. P. Pielou, of the Entomology Research Institute, Ottawa, has obtained a few *coloradella* from sporophores of *Polyporus* and *Fomes* collected from birch in southern Ontario in May after overwintering in the field (Pielou, *in litt.*, 1966; Pielou and Matthewman, 1966). The species has been reared on a number of occasions in connection with the Hopkins collections. The specific larval food in most of these cases is unknown, but in Montana (Hopk. 12 316), Brunner noted that the small, black larvae fed in fresh bark immediately under the layer of rough, old bark on *Pinus ponderosa*. Feeding resulted in a diseased looking area of the cambium, which, however, was not reached by feeding larvae. Some larvae were located in a spot where decay of the bark and cambium had begun. Larvae were also noted to be cannibalistic and predatory on larvae of *Pinipestis* ([= *Dioryctria*], Pyralidae).

The most extensive study of the biology of *B. coloradella* is that of Yothers (1932, 1942), who found the larvae inside the closed, perennial cankers caused by the fungus *Neofabraea* on apple trees. Dead aphids (*Eriosoma*), honeydew, and excreta were massed together with the webbing of the moth larvae. He observed that larvae fed on dead and decaying wood and bark, particularly old, desiccated callus tissue, and did not feed on live callus tissue.

Biological data.—CANADA: ONTARIO: Bell's Corners, r.f. *Polyporus betulinus* on *Betula*, emgd. VI-10-65; r.f. *Fomes fomentarius* on *Betula*, emgd. VI-21-65 (D. P. Pielou). WASHINGTON: PEND OREILLE CO.: Metaline Falls, V-22-31, 2 ♂ ♂ r.f. *Pseudotsuga menziesii* bark (Hopk. 21 309) (W. D. Bedard). MONTANA: MISSOULA CO.: Missoula, II-20-14, 1 ♀ r.f. *Pinus ponderosa* bark, emgd. III-5-14 (Hopk. 12 316) (J. Brunner). IDAHO: VALLEY CO.: Krassel Rgr. Station, 1957, ♂ ♂ ♀ ♀ r.f. *Pseudotsuga menziesii* stems with *Dendroctonus* (Hopk. 35 025 m) (H. M. Furniss); same locality III-28-62, 2 ♀ ♀ r.f. *Alnus* stem infested with Cerambycidae (Hopk. 41 890p) H. M. Furniss); same locality IX-6-62, 1 ♂ 1 ♀ r.f. *Pseudotsuga menziesii* stems with *Dentroctonus*, emgd. III-18-63 (H. M. Furniss). CALIFORNIA: ALAMEDA CO.: Berkeley, V-29-60, 1 ♂ r.f. *Poria versipora* on

Umbellularia californica (J. Lawrence, JFL 581); Berkeley Hills nr. Claremont Cyn., II-10-67, 1 ♀ r.f. *Quercus agrifolia* bark with *Stereum*, emgd. III-21-67 (J. Powell, JAP 67B5); same locality, II-14-67, 1 ♂, 3 ♀ ♀ r.f. *Quercus agrifolia* bark with *Stereum* and log with *Hypoxylon*, emgd. III-19 to IV-20-67 (J. Powell and P. A. Rude, JAP 67B6, B7); Oakland Hills (Redwood Road), II-9-66, 1 ♀ r.f. *Hypoxylon occidentale* [= *H. thouarsianum*] on *Quercus agrifolia*, emgd. V-6-66 (J. Wolf, JAP 66B9). SONOMA CO.: 4 mi. NW Camp Meeker, II-25-66, 1 ♀ r.f. *Stereum hirsutum* on *Lithocarpus*, emgd. V-11-66 (A. J. Slater and J. Wolf, JAP 66B39).

Eumeyrickia trimaculella (Fitch)

Chaetochilus trimaculellus Fitch, 1856, Trans. N. Y. Agric. Soc., 15: 455. (Reprinted, 1856, as separately paged vol., Report on Noxious, Beneficial and other insects, N.Y., II, p. 233).
Eumeyrickia trimaculella; Busck, 1902, Jour. N. Y. Ent. Soc., 10: 94 (synonymy); Clarke, 1941, Proc. U. S. Natl. Mus., 90: 271 (placed in Ethmiidae).
Anarsia? albapulvella Chambers, 1875, Canad. Ent., 7: 147.
Chimbache? haustellata Walsingham, 1882, Trans. Amer. Ent. Soc. Phila., 10: 173.

As mentioned in connection with the preceding species, assessment of structural characters of *E. trimaculella* in connection with current studies on the Ethmiidae indicate that this species should be referred to the Oecophoridae, in contrast to the opinion of Clarke (1941).

Details of the biology of this insect have not been reported, but it is a fungus feeder, at least at times, which lends credence to the supposed relationship with the Oecophoridae. Fitch (1856) found *trimaculella* in yards about houses and mentioned its oviposition habits but did not state upon what substrate the eggs were deposited. The moths were noted to favor hollow trees by Forbes (1923), but evidently no larval food was known then. Through the cooperation of D. P. Pielou, of the Entomology Research Institute, Ottawa, we have been able to examine specimens of *E. trimaculella* which he has reared in connection with investigations on the insect community of *Polyporus betulinus* and *Fomes fomentarius* on birch (Pielou, 1966; Pielou and Matthewman, 1966). Sporophores which had overwintered in the field were collected in May and June.

Biological data.—CANADA: QUEBEC, Gatineau Park, r.f. *Polyporus betulinus*, emgd. VI-10-65; r.f. *Fomes fomentarius*, emgd. VII-15, VIII-5-65 (D. Pielou). VERMONT: BENNINGTON CO.: East Dorset, VI-6-65, 1 ♂ r.f. undet. fungus (C. Parsons, JFL 1715); Green Peak, 2000 ft., East Dorset, VI-6-65, 1 ♀ r.f. *Fomes fomentarius* on *Betula lutea* (C. Parsons, JFL 1707).

OINOPHILIDAE

Oinophila v-flava (Haworth)

Gracillaria v-flava Haworth, 1811, Lepid. Britannica, 4: 530.
Oinophila v-flava; Stephens, 1848, Proc. Ent. Soc. London, 5(5): lxi.

As discussed elsewhere, this species is thought to have been introduced into California from Europe (Powell, 1964a). The habits are poorly known and *O. v-flava* may be a general scavenger, but it appears that feeding usually takes place on some fungus, such as on a moldy substrate.

Biological data.—CALIFORNIA: ALAMEDA CO.: Berkeley Hills nr. Claremont Cyn., II-14-67, 2 ♂ ♂, 2 ♀ ♀ r.f. bark *Quercus agrifolia* with *Stereum* and *Hypoxylon*, emgd. III-16 to IV-3-67 (J. Powell and P. A. Rude, JAP 67B6, B7). SANTA BARBARA CO.: Prisoner's Harbor, Santa Cruz Island, IV-29-66, 1 ♂ as adult on *Polyporus gilvus* on *Quercus agrifolia*, emgd. VIII-2, VIII-12-66 (J. Powell, A. Slater, J. Wolf, JAP 66E8). SANTA CLARA CO.: San Jose, XI-30-59, ♂ ♂ ♀ ♀ r.f. moldy bark of flowering locust, emgd. I-18 to II-8-60 (L. B. McNelly, JAP 60A2).

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The Zoogeography of Lesser Antillean *Anolis* Lizards—An Analysis Based Upon Chromosomes and Lactic Dehydrogenases

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THE ZOOGEOGRAPHY OF LESSER ANTILLEAN *ANOLIS* LIZARDS—AN ANALYSIS BASED UPON CHROMOSOMES AND LACTIC DEHYDROGENASES[1]

GEORGE C. GORMAN[2] AND LEONARD ATKINS[3]

ABSTRACT

On each island bank of the Lesser Antilles, there are one or two distinct forms of iguanid lizards of the genus *Anolis*. On the basis of osteology, these anoles have been placed in two species groups, which show a sharp geographic break. The southern group (termed *roquet*) occupies all the islands from Grenada north to Martinique. The northern group (called *bimaculatus*) is found from Dominica, the island due north of Martinique, on through all the other Lesser Antillean islands. It also occurs on several of the Greater Antillean islands and island banks.

Differences in karyotype and in electrophoretic mobility of the protein lactic dehydrogenase amongst these Antillean lizards have permitted a detailed analysis of relationships, evolutionary history, and zoogeographic movement. The two species groups are distinct osteologically, chromosomally, and biochemically. The *roquet* group is characterized by 12 metacentric macrochromosomes, 22 or 24 microchromosomes, and the absence of sex chromosomal heteromorphism. This karyotype appears to be primitive for the family Iguanidae and characterizes many genera, including a South American anoline genus. The lactic dehydrogenases of the *roquet* group are characterized by very slow anodal migration in borate buffer. The *bimaculatus* group is characterized by a reduced number of chromosomes, a less sharply marked break between macro- and microchromosomes, and male heteromorphism. Their lactic dehydrogenases migrate more rapidly towards the anode than do those of the *roquet* group.

Three subgroups of *bimaculatus* may be recognized; two are strictly Lesser Antillean and are characterized by 9 or 10 pairs of macrochromosomes, with no sharp break between the sixth and seventh pair. In the first of these, the *bimaculatus* group *sensu stricto*, all members have identical LDH mobilities. The second, *wattsi*, has only one species; in karyotype it is identical to most *bimaculatus*, but has a more rapidly migrating LDH. The third subgroup is found to the west of the Lesser Antilles on St. Croix, Puerto Rico, and Hispaniola. It is termed the *acutus* group. The LDH of *wattsi* is identical to that of two members of the *acutus* group. In chromosomes, the *acutus* group appears somewhat intermediate to the karyotypically primitive *roquet* group in the south, and its near-neighbor

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wattsi and *bimaculatus* groups. Like the *roquet* group, *acutus* has six pairs of metacentric macrochromosomes, and the majority of the species have a sharp break between pairs six and seven. However, pair seven is not truly small enough to be called microchromosomal; it is intermediate in size. There is a sharp break between pair seven and the microchromosomes. Like the *bimaculatus* group, the *acutus* group is characterized by male chromosomal heteromorphism, and a male diploid number of 33 or less.

The karyotypes of some species of *Anolis* on Puerto Rico and Hispaniola are identical to that of the *roquet* group. It is argued that there were two colonizations of the Antilles from South America, one to the southern Lesser Antilles, ultimately giving rise to the *roquet* group; the second to the Greater Antilles. In the Greater Antilles, one stock arose that evolved a reduced diploid number and male heteromorphism. This group gave rise to the *bimaculatus* group, which became established in the northern Lesser Antilles. Furthermore, it is postulated that the *roquet* and *bimaculatus* groups were colonizing the Lesser Antilles at approximately the same time from opposite directions. The non-overlap between the two groups is due to competitive exclusion.

INTRODUCTION

On virtually every island in the Caribbean, there is at least one and sometimes as many as 25 species of small to moderate sized lizards of the genus *Anolis* (Fig. 1). This genus has always been difficult for systematists. In the preface to a series of papers on the anoles of the Lesser Antilles, Williams (1959: 188) wrote, "The segment of *Anolis* that is here reported on was believed to be, and may well be, the simplest areal segment of the genus in which more than one species occurs. . . . Yet we have found the complications formidable and not amenable to study on the basis of preserved specimens alone." Further, on the same page Williams stated, "It is even more evident in this genus than in others that we cannot be prisoners of our conventional museum techniques, that a very wide approach will barely encompass the things we need to know." In this paper we escape from the "prison" of conventional museum techniques by entering the laboratory.

We chose to investigate biochemical and cytological characters because they provide an independent check on morphological characters and, quite simply, because they work. In a study of the relationships of the anoles of the southern portion of the Lesser Antilles (Gorman and Dessauer, 1966), we noted that lactic dehydrogenase (LDH) defined the *roquet* group: electrophoretic properties common to the LDHs of the *roquet* species group differed from those of all other anoles studied. Likewise, chromosome studies on *Anolis* (Gorman, 1965; Gorman and Atkins, 1966, 1967) indicated the value of karyotype as a systematic character. In our discussion of the northern Lesser Antillean anoles we shall rely primarily on these two characters. In tracing the biogeographic movements of the southern species group, we shall also utilize other information available to us.

GEOGRAPHY

The Lesser Antilles are the chain of Caribbean islands stretching from St. Croix south to Grenada. These are oceanic islands, never having been connected to the main continental land masses. On each of these numerous islands are found one or two native species of *Anolis*—a genus of lizard that has been outstandingly successful in colonizing the Caribbean. Some of the islands of the Lesser Antilles were once parts of larger islands only recently fragmented, and, as pointed out by Baskin and Williams (1966), "in treating the zoogeography of the Lesser Antilles, we must deal with the banks and not solely the present islands." As will be seen, each bank has at least one endemic form, and only one form has been

Figure 1. *Anolis roquet roquet* from Martinique. An adult male with throat fan extended in territorial display.

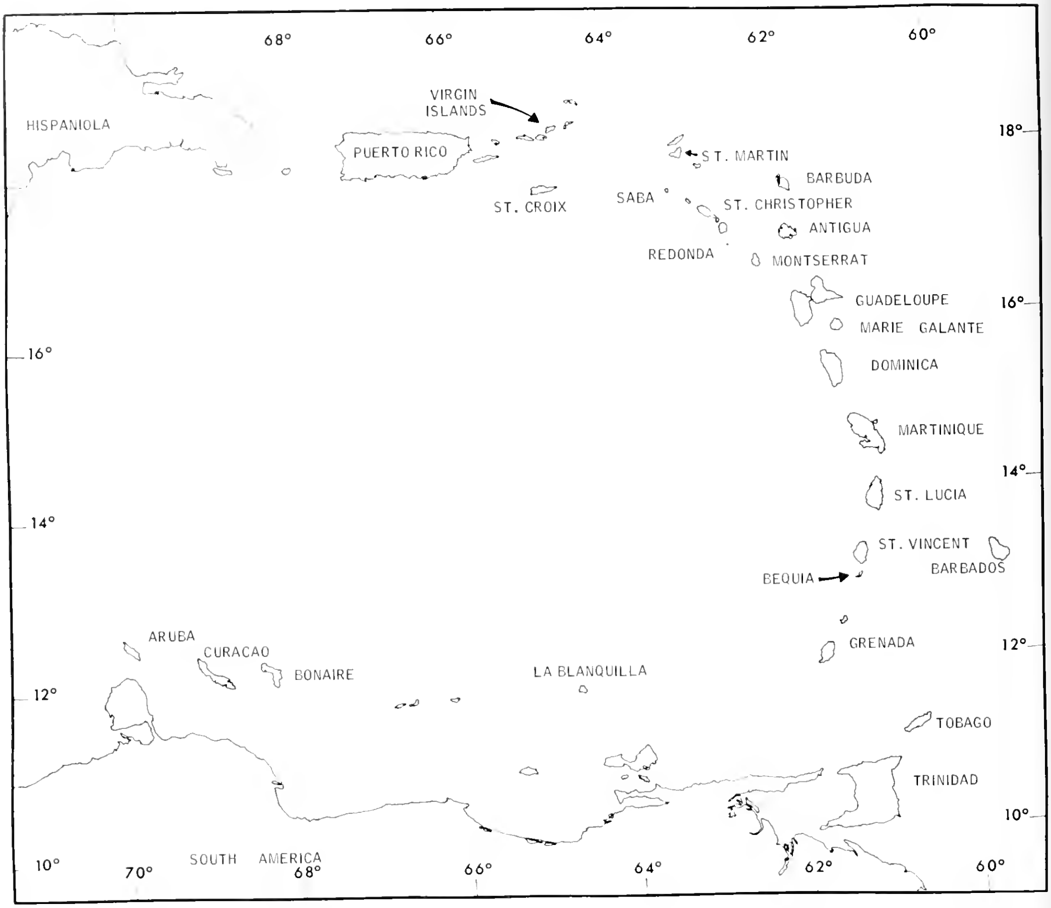


Figure 2. Map of the eastern Caribbean. The Lesser Antilles extend from St. Croix in the north to Grenoda in the south.

successful in establishing itself on more than one island bank.

Two types of islands may be distinguished grossly in this archipelago: steep, montane, volcanic islands, which have high rainfall in at least some parts and are ringed either by steep cliffs or beaches of white or black sand; and low, flat, relatively xeric, limestone islands, ringed by white sand beaches only. These flat islands, presumably older, lie to the east of the montane islands and are sometimes called the outer chain. The southern limit of this outer chain is Marie Galante and the Grande Terre portion of Guadeloupe. It includes the Antigua bank and the Anguilla bank. Guadeloupe itself is actually a double island; the western half is very mountainous. The mountainous chain begins in Grenada and continues north through Saba. Lying somewhat to the east of the main Lesser Antillean double chain is Barbados—also a relatively flat island with little topographic variation. Figure 2 shows the Lesser Antillean chain.

The *Anolis* on these islands fall into distinct species groups. Underwood (1959) called the group occupying the southern islands (from Grenada north to Martinique) the *roquet* group; those anoles on the northern islands were placed in the *bimaculatus* group. The groups were recog-

nized as distinct by Underwood, but the characters used to separate them were trivial, *e.g.*, "in the *bimaculatus* group [the canthal ridge] is followed by a series of differentiated small supraciliaries; in the *roquet* group there is no differentiated series of small supraciliaries." And, "the caudal scales are arranged in whorls corresponding to the autotomy septa; in the *bimaculatus* group there are three or four dorsal crest scales in each whorl; in the *roquet* group there are usually five . . . if there are less it is only as an individual variation and not as a population character" (p. 193).

However, work by Etheridge (1960) and by Gorman and co-workers showed that the two major groups were quite distantly related. The *roquet* group was not recognized *per se* by Etheridge; all species within the group were placed in the *latifrons* series, a predominantly South American and presumably primitive series. Etheridge's concept of the *bimaculatus* group includes species in the northern Lesser Antilles, the Puerto Rico bank, Hispaniola, and the Bahamas. The two Lesser Antillean species groups differ profoundly in karyotype (Gorman and Atkins, 1967), display behavior (Gorman, 1968), and lactic dehydrogenase mobility in starch gel electrophoresis (Gorman and Dessauer, 1966). They are not closely related. That Underwood had to rely on trivial external characters to separate the groups emphasizes the fact that these two groups occupy virtually identical niches on islands of similar size and have thus been subject to similar selective pressures.

Our chromosome data are concordant with Etheridge's osteological data in that they indicate that the *roquet* group is primitive and the *bimaculatus* group more highly specialized (see Gorman, Atkins, and Holzinger, 1967; Gorman and Atkins, 1967)

Within the *bimaculatus* group in the Lesser Antilles, Underwood (*op. cit.*) singled out *wattsi* as being quite distinct in several characters, and he placed this species in a group of its own. We, too, shall refer to the *wattsi* group. In addition, those members of the *bimaculatus* group *sensu* Etheridge that occur in the Greater Antilles and that were not considered by Underwood shall be called the *acutus* group. Etheridge's *bimaculatus* group will then consist of three elements: (1) the *bimaculatus* group *sensu stricto;* (2) the *wattsi* group; (3) the *acutus* group.

On Curaçao, to the west of Bonaire, and on the continental island of Trinidad are two species of a predominantly South American species group (*chrysolepis* group) that will not be reconsidered here (see Gorman and Atkins, 1967).

TAXONOMY

As Underwood wrote in 1959, "These lizards present the familiar nomenclatorial problem of island populations. Given a full knowledge of the relevant facts, which we certainly do not have, there remains a considerable element of personal taste in deciding how to represent them nomenclatorially." Since that time, the *roquet* species group has been intensively studied, and we are somewhat more confident about species relationships. Comparable studies have not been undertaken for the *bimaculatus* group. Underwood (1959) placed most of the island races as subspecies of *bimaculatus*. Lazell (1962 and 1964a) studied intra-island variation in the *bimaculatus* group of Dominica and Guadeloupe and named intra-island subspecies of *oculatus* and *marmoratus*, respectively. (The latter also has subspecies that occur on the islands satellite to Guadeloupe.) This report is not concerned with nomenclatorial designation. For the *bimaculatus* group we shall simply use the name of the form that is characteristic for a given island bank; we shall disregard Lazell's intra-island subspecific designations and shall not be concerned with whether Underwood considered the given form a subspecies of *bimaculatus* or a species. The *wattsi* group offers no problems—there is only one species and no named subspecies (*Anolis alter*, Williams,

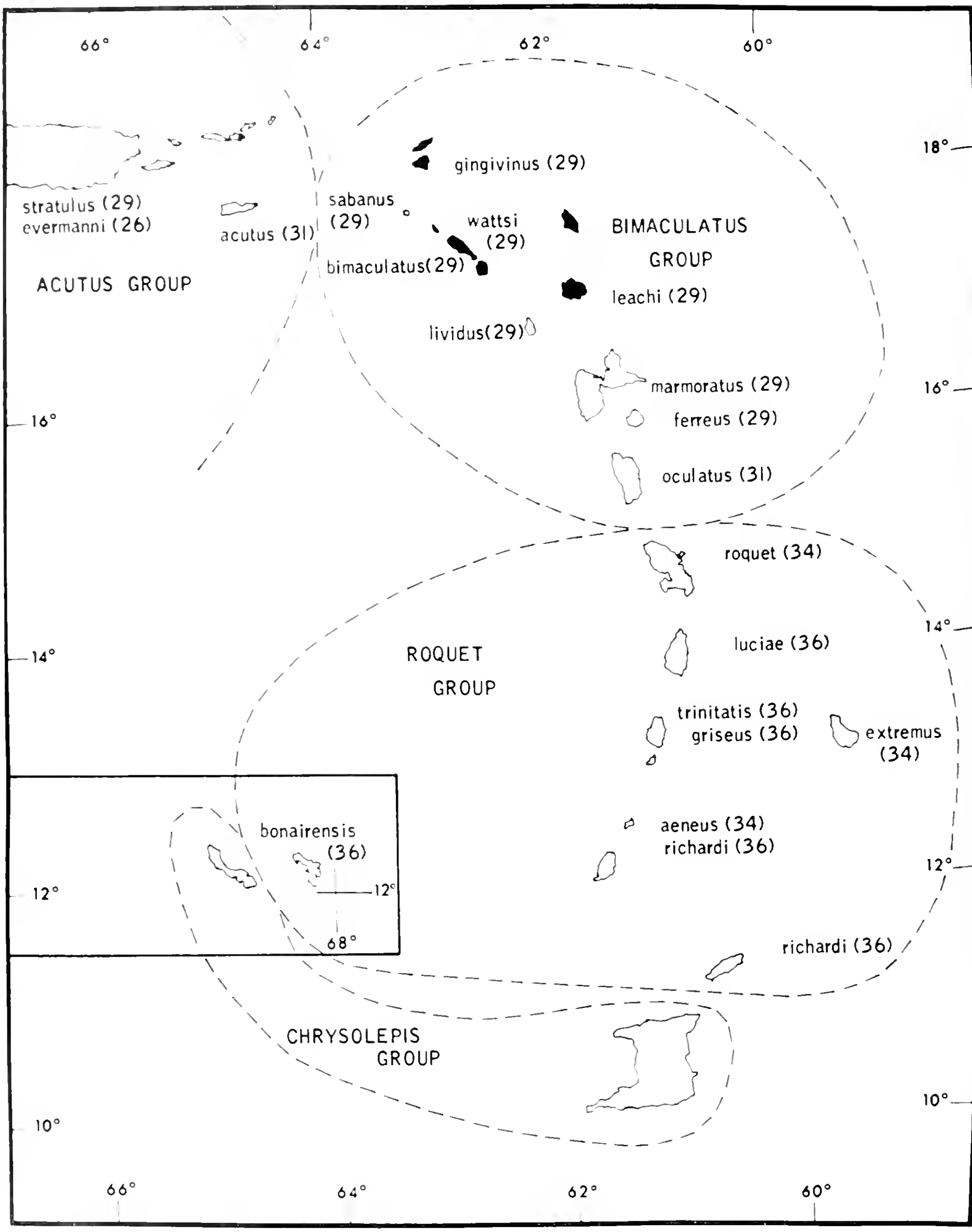


Figure 3. The distribution of Lesser Antillean *Anolis*. Species groups are separated by broken lines. The western part of the range is inset in solid lines. Numbers in parentheses are diploid chromosome counts for males. Names of forms are adjacent to the islands on which they occur. Only one species, *wattsi*, is found on more than one Lesser Antillean bank; its distribution is indicated by black islands. On each of these islands, *wattsi* is sympatric with a *bimaculatus* group form. In addition, *richardi* is found not only on the Grenada bank, but on Tobago, which geologically is not part of the Lesser Antilles. One member of the *acutus* group, *Anolis distichus* (2n = 33), is found on Hispaniola, the Bahamas, and Florida, north and west of the area included on the map.

1962, is a synonym of *wattsi*: Williams, personal communication). The *acutus* group also offers no problems, as the species are well defined. Names for the *roquet* group will follow Gorman and Dessauer (1966).

The distribution of these species groups and the forms considered are illustrated in Figure 3.

The important points illustrated by this figure are:

(1) There is complete exclusion between the *roquet* group and the *bimaculatus* group. (2) The break between the two groups falls between Martinique and Dominica. (3) There is nothing geologically "natural" about this break, *i.e.*, it has nothing to do with the inner chain and outer chain. (4) Only one Lesser Antillean form, *wattsi*, has successfully colonized more than one island bank.

MATERIALS AND METHODS

Chromosomes were studied either by direct preparation of gonads for meiotic as well as mitotic cells, or by tissue culture of blood or lung, following Gorman and Atkins (1966).

To study LDH, crude extracts of hearts were made by grinding fresh or frozen tissue in a glass tissue grinder. Hearts from a population were from either a single animal or pooled samples. This made no difference, as we have found no intrapopulational variation in electrophoretic mobilities of heart LDH. The tissue was ground in a 0.25 M sucrose solution. No effort was made to maintain a constant tissue weight/volume of solution. Approximately 2 ml of sucrose were used per 0.05 grams of heart. The extracts were then compared by means of starch-gel electrophoresis, following the outlined procedure of Fine and Costello (1963).

Tissue LDH of anoles, as of many other animals, shows five distinct electrophoretic bands (Gorman and Dessauer, 1966). These result from the tetrameric association of hybrids of two distinct proteins termed heart (H) LDH and muscle (M) LDH. Thus the five bands represent H_4, H_3M, H_2M_2, HM_3, and M_4 (Salthe *et al.*, 1965). The two types H and M are so named because they predominate in those tissues. In this study all results are based upon differences in the mobilities of the H_4 LDH, which were more striking than differences found in the more slowly migrating M_4 LDH.

RESULTS

Roquet group

The chromosomes of the *roquet* group have already been discussed (Gorman and Atkins, 1967). Five forms, *luciae, trinitatis, bonairensis, griseus,* and *richardi*, have six pairs of metacentric macrochromosomes and twelve pairs of microchromosomes ($n=18$, $2n=36$). The other three forms, *aeneus, roquet,* and *extremus*, have a similar macrochromosomal complement, but only eleven pairs of microchromosomes ($n=17$, $2n=34$). There is no evidence of sex chromosomal heteromorphism.

The biochemical study on the *roquet* group (Gorman and Dessauer, 1966) indicated that the group was characterized by an anodally slow LDH. This work was based upon LDH in red blood cells, and resolution was not clear. Comparison of heart LDHs shows that seven forms have an electrophoretically identical LDH, while *richardi* (Grenada bank and Tobago) has an LDH of slightly faster anodal mobility (Fig. 4).

Bimaculatus group *sensu stricto*

The karyotype of the *bimaculatus* group differs considerably from that of the *roquet* group. It was in this species group that sex chromosomes in lizards were first demonstrated (Gorman and Atkins, 1966). Our original report showed that *bimaculatus, leachi, ferreus,* and *gingivinus* were all characterized by male $2n=29$, female $2n=30$. In meiosis of the male, there are 9 large bivalents decreasing gradually in size, 4 microbivalents, and a sex trivalent. In mito-

Figures 4 and 5. Heart lactic dehydrogenases of Lesser Antillean anoles. Drawings from starch gels. Each figure is a composite of several electrophoretic runs. Only samples on the same gel may be compared directly, as different gels were run for different lengths of time. All migration is anodal (toward the +). Site of sample application is marked by horizontal line below code letter. Small vertical bars separate individual gels.

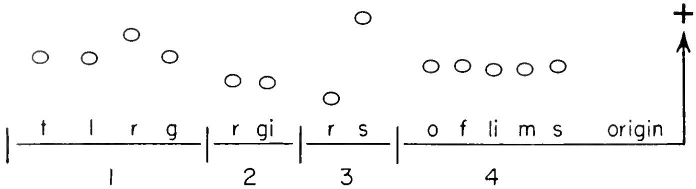


Figure 4. Gel 1. The *roquet* group. Phosphate buffer pH 7.0; t, *trinitatis*; l, *luciae*; r, *richardi*; g, *griseus*. All members of the group have identical LDH mobility except for *richardi*, which is slightly faster. Gel 2. Comparison of *richardi* (r), the "fastest" of the *roquet* group, with *gingivinus* (gi) of the *bimaculatus* group. Phosphate buffer pH 7.0. Migration rates approximately equal. Gel 3. Comparison of *richardi* (r) with *sabanus* (s) of the *bimaculatus* group. Borate buffer pH 8.6. In borate buffer the *roquet* group is characterized by very slow anodal migration. Gel 4. The *bimaculatus* group. Phosphate buffer pH 7.0. All members have identical LDH mobility. Shown here are *oculatus* (o), *fereus* (f), *lividus* (li), *marmoratus* (m), and *sabanus* (s).

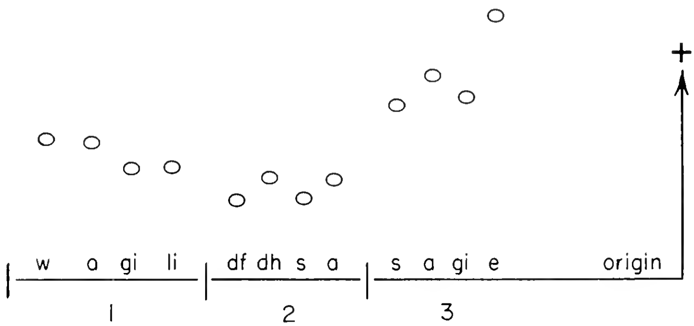


Figure 5. All phosphate buffer pH 7.0. Gel 1. Comparison of *wattsi* and *acutus* with *bimaculatus* group. Both *wattsi* (w) and *acutus* (a) have faster anodal migration than the members of the *bimaculatus* group (illustrated are *gingivinus* (gi) and *lividus* (li)). Gel 2. LDH variation in the *acutus* group. Interspecific variation in *distichus* from Florida (df) and Haiti (dh). The mobility of *stratulus* (s) falls between these two; *acutus* (a) appears identical to *distichus* from Haiti. Gel 3. Comparison of *acutus* and *bimaculatus* groups. The fastest LDH mobility is that of *evermanni* (e). The mobility of the *bimaculatus* group, represented by *gingivinus* (gi), is intermediate to that of *acutus* (a) and *stratulus* (s).

sis there are thus 13 pairs of chromosomes, and three unpaired chromosomes, an acrocentric X_1, microchromosome X_2, and a metacentric Y. Females are $X_1X_1X_2X_2$. Meiosis in females has not been studied. Further study of *sabanus, marmoratus*, and *lividus* shows these to be quite similar to those previously cited. Only one member of the *bimaculatus* group differs in karyotype: *A. oculatus* from Dominica, the southernmost island inhabited by this group. As already reported (Gorman and Atkins, 1967), *oculatus* has a similar sex chromosomal mechanism but a higher number of autosomes (male 2n=31, female 2n=32). The difference appears to be Robertsonian—one pair of small metacentric macrochromosomes present in all other members of the *bimaculatus* group is represented by two pairs of acrocentric chromosomes in *A. oculatus*. Figures 6A and B compare meiotic chromosomes in two members of the *bimaculatus* group, and Figures 7A and B compare mitotic karyotypes in two forms.

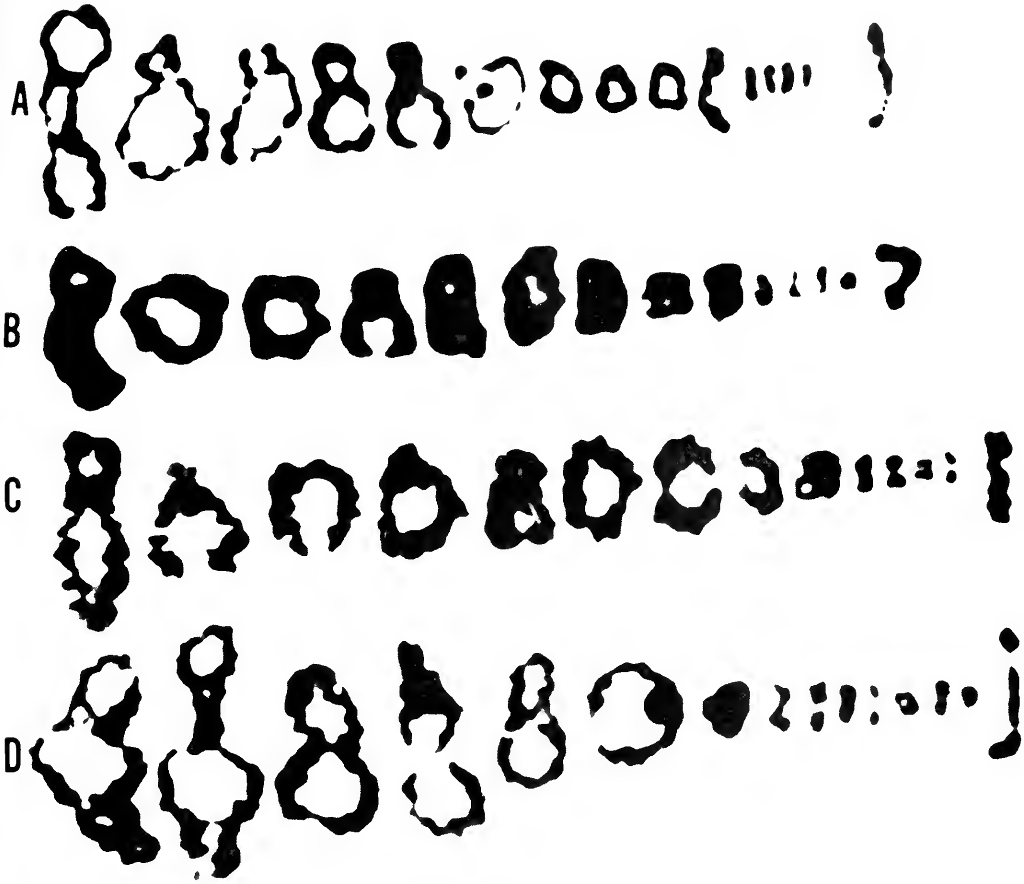


Figure 6. Diakinesis in males of the *bimaculatus*, *wattsi*, and *acutus* groups. A.—*oculatus* (*bimaculatus* group). There are 15 bodies, 14 bivalents and a sex trivalent on the far right. The thin thread connecting one element of the trivalent has been retouched with two dots of ink (republished with permission from Systematic Zoology). B.—*sabanus* (*bimaculatus* group). There are 13 bivalents, and a sex trivalent on the far right. C.—*wattsi* (*wattsi* group). Virtually identical to *sabanus*. D.—*acutus* (*acutus* group). There are 14 bivalents, and a sex trivalent on the far right. Giemsa stain in all chromosome preparations.

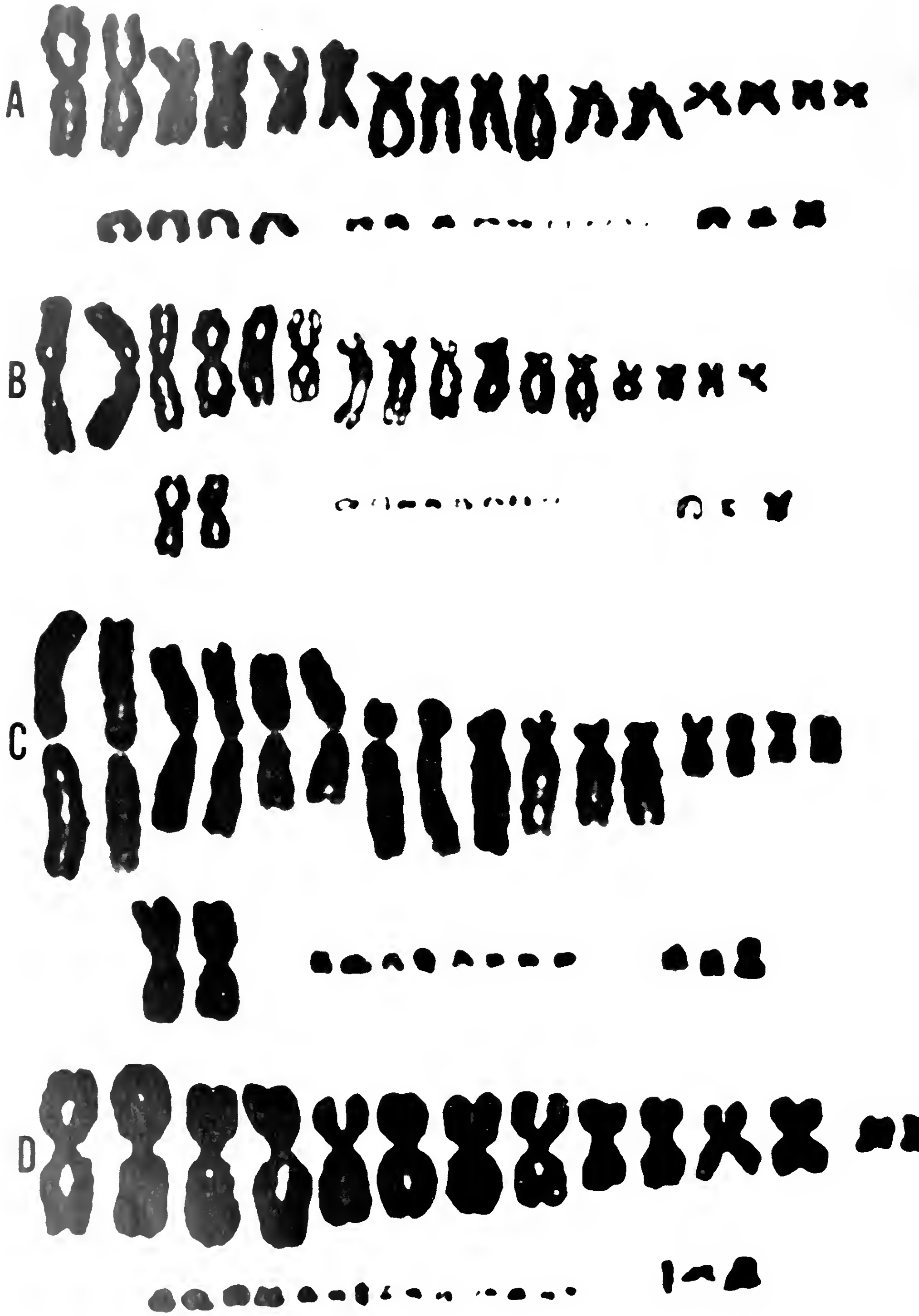
All members of the *bimaculatus* group have identical H LDH electrophoretic mobility. The LDH of *richardi*, the fastest migrating LDH in the *roquet* group, is approximately equal in mobility to that of the *bimaculatus* group in phosphate buffer gel (pH 7). However, in borate buffer (pH 8.6), the LDH of *richardi* and those of all members of the *roquet* group have relatively slow anodal mobility; the LDH band is well behind that of the *bimaculatus* group (Fig. 4).

Wattsi group

We have compared *wattsi* from St. Martin and Antigua and have found no differences in karyotype and LDH mobility. The karyotype of *wattsi* appears virtually identical with that of typical *bimaculatus* (Fig. 6C). In LDH, the mobility is slightly faster than in the *bimaculatus* group (Fig. 5).

Acutus group

The species of this group do not form a tight unit—neither in LDH nor in chromo-


A
B
C
D

somes—and each will be discussed separately.

A. acutus (St. Croix): The heart LDH mobility of this species appears identical with that of *wattsi* (Fig. 4). The karyotype however, differs from that of *wattsi* and of all other anoles previously described. In meiosis there are 14 autosomal bivalents and one sex trivalent, 2n=31. While this number in itself is not different from that of *A. oculatus* of the *bimaculatus* group *sensu stricto*, the morphology of the chromosomes is quite different. There are six large pairs of metacentric macrochromosomes, and then a small seventh pair somewhat intermediate in size between the macro- and microchromosomes. There are eight pairs of microchromosomes, one of which must represent the X_1 and X_2, and there is an unpaired small metacentric Y. Whether the X_1 and X_2 are heteromorphic, as is the case in typical *bimaculatus* anoles, could not be ascertained. No females were available for study. Figures 6D and 7D illustrate meiotic and mitotic chromosomes.

A. distichus: Lizards from Bimini, New Providence (Bahamas), Florida (introduced population), and Port-au-Prince, Haiti, were studied. There are 15 bivalents and a sex trivalent at meiosis (Fig. 9E); male 2n=33, female 2n=34. This a formula unique among the anoles studied by us to date (more than 70 species and subspecies). The macrochromosomal complement consists of seven pairs of metacentric or slightly submetacentric chromosomes. However, in this case, there is a sharp break in size between pairs 5 and 6, whereas in the other members of the *acutus* group and in the *roquet* group the break comes between pairs 6 and 7. Both sexes have eight pairs of microchromosomes. The male has three unpaired sex chromosomes, a submetacentric Y and two heteromorphic acrocentrics (X_1 and X_2) (Fig. 7A); the female is $X_1X_1X_2X_2$.

In LDH there has been interpopulation differentiation. Hispaniolan *distichus* has a rapidly migrating H LDH that appears identical to those of *acutus* and *wattsi*, whereas specimens from Bimini and Florida populations have slower anodal mobility (Fig. 4).

A. stratulus (Puerto Rico): At meiosis there are 13 bivalents and one sex trivalent (Fig. 9D), male 2n=29 (Fig. 8B). While this count is like typical *bimaculatus*, again the karyotype is quite unique. In mitotic metaphase there are six pairs of metacentric macrochromosomes and a sharp break between pairs six and seven; the seventh pair is also metacentric, being somewhat intermediate in size between the macrochromosomes and the six pairs of microchromosomes. In males there are three unpaired sex chromosomes. Females have not been available for study. In H LDH, the mobility is slower than in *acutus* and slightly faster than in Bahaman *distichus* (Fig. 5).

A. evermanni (Puerto Rico): This anole is most distinct both in karyotype and LDH mobility. It has the most rapidly migrating H LDH, the mobility being approximately 1.5 times faster than that of *acutus* (Fig. 5). In chromosomal formula it is also unique (Gorman and Atkins, 1968a). It is the only member of the *bimaculatus* group *sensu lato* that does not have the X_1X_2Y

←

Figure 7. Karyotypes in males of the *bimaculatus*, *wattsi*, and *acutus* groups. A.—*oculatus* (*bimaculatus* group). 2n = 31. There are 28 autosomes and three unpaired sex chromosomes (shown on the far right of the second row). Leukocyte culture. B.—*fereus* (*bimaculatus* group). 2n = 29. There are 26 autosomes and three unpaired sex chromosomes (far right of second row). Note the marked similarity in the autosomes of *fereus* and *oculatus* except that two pairs of acrocentric chromosomes of *oculatus* (far left second row) correspond to one pair of metacentrics in *fereus*. Leukocyte culture (republished with permission from American Naturalist). C.—*wattsi* (*wattsi* group). 2n = 29. Virtually identical to *fereus* above. Direct testis preparation. D.—*acutus* (*acutus* group). 2n = 31. There are 28 autosomes and three unpaired sex chromosomes (shown on far right of second row). Leukocyte culture.

Figure 8. Koryotypes in males of the *acutus* group. A.—*distichus*. 2n = 33. There are 30 autosomes and three unpaired sex chromosomes (shown on far right of second row). Leukocyte culture. B.—*stratulus*. 2n = 29. There are 26 autosomes and three unpaired sex chromosomes (far right of second row). Direct testis preparation. C.—*evermanni*. 2n = 26. This is the only member of the *bimaculatus* group with a heteromorphic *pair* of sex chromosomes (far right of second row). This is also the lowest diploid number reported in the genus *Anolis*.

sex chromosome system. Both males and females have diploid numbers of 26. However, in the male there is a heteromorphic pair of acrocentric chromosomes (Fig. 8C). As in *acutus* and *stratulus*, the six largest macrochromosomes are meta- or submetacentric; there is a sharp break in size between pairs six and seven, and pair seven is also clearly metacentric. The sex chromosomes are the eighth pair.

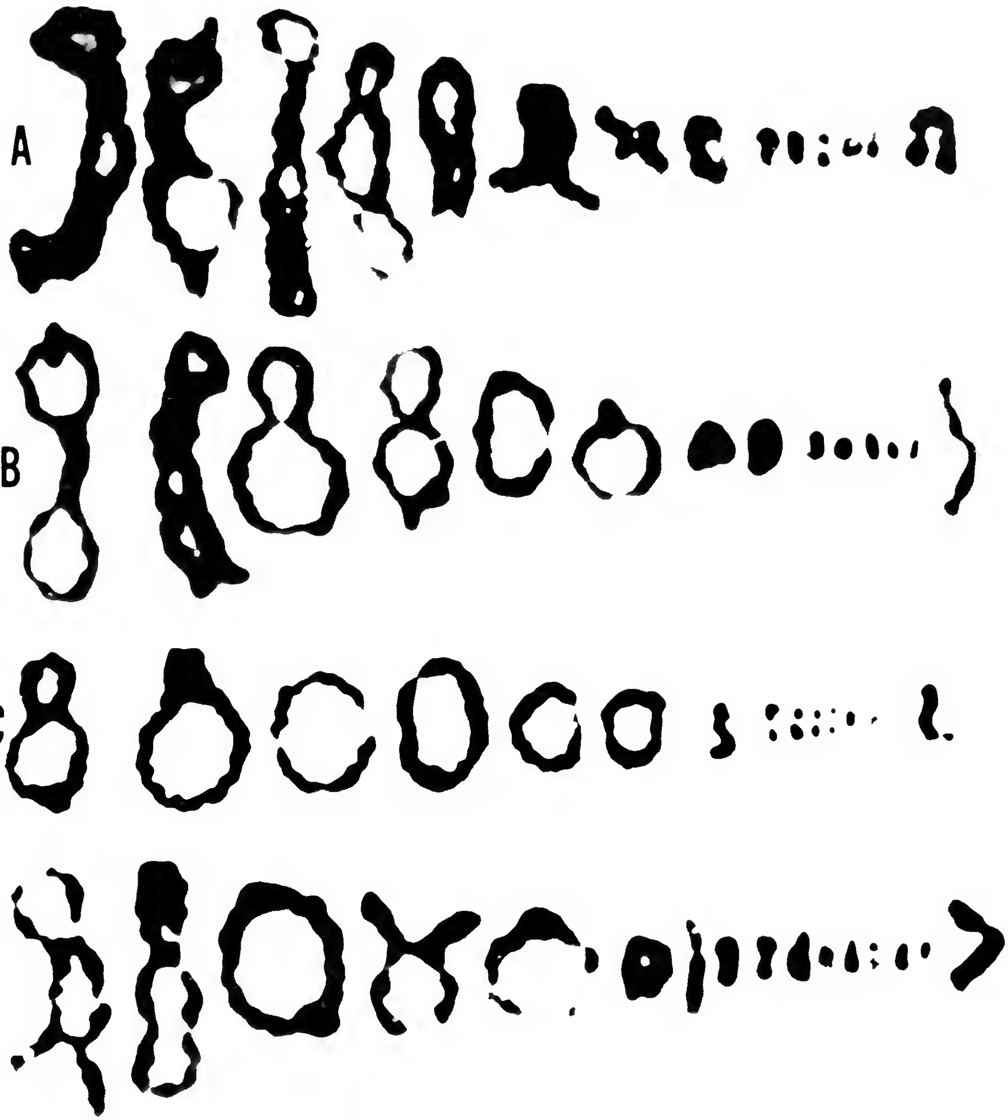


Figure 9. Diakinesis in males of the *cristatellus* and *acutus* groups. A.—*pulchellus;* B.—*gundlachi* (both *cristatellus* group). Each has six macro-, two intermediate, and five micro-bivalents; a sex trivalent is shown on the far right. C.—*stratulus* (*acutus* group). There are six macro-, one intermediate, and six micro-bivalents; a sex trivalent is shown on the far right. D.—*distichus* (*acutus* group). There are five macro-, two intermediate, and eight micro-bivalents; a sex trivalent is shown on the far right.

Chromosomal data on other Puerto Rican anoles

For comparative purposes, it is important to consider the information available on other Puerto Rican anoles. There are ten species on the island. Two of these (*evermanni* and *stratulus*) belong to the *acutus* series and were discussed above. Six other species are placed by Etheridge in the *cristatellus* group, which he considers closely

Figure 10. Karyotypes of Puerto Rican *Anolis*. A.—*cuvieri* female. 2n = 36. There are six pairs of metacentric macrochromosomes (top row), and 12 pairs of microchromosomes (second row). Males appear identical. There are no obvious heteromorphic sex chromosomes. Leukocyte culture. B.—*pulchellus* (*cristatellus* group) male. 2n = 29. As in the above, there are six pairs of metacentric macrochromosomes. There is not a sharp break between macro- and microchromosomes. There are two intermediate sized pairs of metacentric chromosomes and five pairs of microchromosomes. There are three unpaired sex chromosomes (far right of second row). Two faintly stained microchromosomes were retouched with ink.

related to, and perhaps derived from, *bimaculatus*. The chromosomes of all the Puerto Rican members of the *cristatellus* group have now been studied. *A. cooki* and *A. cristatellus* were discussed in a recent paper (Gorman, Thomas, and Atkins, 1968). The diploid numbers for males are 29 and 27 respectively. Details will not be repeated here. The other four species[1] have karyotypes virtually identical to one another and quite similar to that of *A. cooki*. In meiosis there are six large bivalents, then a sharp break and two intermediate sized bivalents, five microbivalents, and an elongate sex trivalent. Figures 9A and B illustrate diakinesis in two forms (*gundlachi* and *pulchellus*). The diploid number in males is 29 (Fig. 10B); we have not studied females.

The *cristatellus* group resembles several members of the *acutus* group in having six pairs of metacentric macrochromosomes with a sharp break in size between pairs six and seven, the smaller seventh pair also metacentric, and an X_1X_2Y sex chromosome system. The only difference, in fact, is that in the *cristatellus* group pair eight is also metacentric (compare Figs. 10B, 8A, B).

Only two other species of *Anolis* occur on Puerto Rico: one is a giant, *A. cuvieri*, the other a dwarf, *A. occultus*. Both are relatively poorly known; *occultus* was only discovered in 1962. Both species have the typical alpha *Anolis* chromosome comple-

[1] *A. gundlachi*, *A. krugi*, *A. poncensis*, *A. pulchellus*.

Table 1. The forms studied and the localities from which they were obtained. The LDH data are tabulated into two major groups, "ro" and "bim." They are distinguished by their migration patterns in the alkaline borate buffer, pH 8.6: "ro" is characterized by slow anodal migration; all "bim" migrate more rapidly. Relative rates of migration follow the major group code. Higher numbers indicate more rapid anodal mobility in starch gel electrophoresis.

Species group	Form	Island locality	Male diploid chromosome no.	LDH
roquet	*roquet*	Martinique	34	ro-1
"	*extremus*	Barbados	34	ro-1
"	*aeneus*	Grenada	34	ro-1
"	*luciae*	St. Lucia	36	ro-1
"	*bonairensis*	Bonaire	36	ro-1
"	*trinitatis*	St. Vincent	36	ro-1
"	*griseus*	St. Vincent	36	ro-1
"	*richardi*	Grenada	36	ro-2
bimaculatus	*lividus*	Montserrat	29	bim-3
"	*sabanus*	Saba	29	bim-3
"	*ferreus*	Marie Galante	29	bim-3
"	*marmoratus*	Guadeloupe	29	bim-3
"	*bimaculatus*	St. Christopher	29	bim-3
"	*leachi*	Antigua	29	bim-3
"	*gingivinus*	St. Martin	29	bim-3
"	*oculatus*	Dominica	31	bim-3
wattsi	*wattsi*	St. Martin and Antigua	29	bim-4
acutus	*acutus*	St. Croix	31	bim-4
"	*distichus*	Haiti	33	bim-4
"	*distichus*	Bahamas	33	bim-1
"	*stratulus*	Puerto Rico	29	bim-2
"	*evermanni*	Puerto Rico	26	bim-5
cristatellus	*cooki*	Puerto Rico	29	not studied
"	*pulchellus*	Puerto Rico	29	not studied
"	*poncensis*	Puerto Rico	29	not studied
"	*gundlachi*	Puerto Rico	29	not studied
"	*krugi*	Puerto Rico	29	not studied
"	*cristatellus*	Puerto Rico	27	not studied
Primitive alpha	*occultus*	Puerto Rico	36	not studied
" "	*cuvieri*	Puerto Rico	36	not studied

ments. Study of mitosis in a female *cuvieri* revealed a karyotype of six pairs of metacentric macrochromosomes and twelve pairs of microchromosomes, 2n=36 (Fig. 10A). We have seen only a few mitotic divisions in *A. occultus;* there are clearly twelve metacentric macrochromosomes, but the number of microchromosomes could not be determined accurately. However, in diakinesis there are clearly six large and twelve small bivalents.

Distributional and karyotypic data for the *wattsi*, *acutus*, and Puerto Rican species groups are illustrated on Figure 11. All data are summarized in Table 1.

DISCUSSION

General

Geologists have not provided us with much useful information about the age of the Lesser Antillean islands. In particular, some of the small islands may have had several cycles above and below the sea, but of this we can say little. Woodring (1954), in a general review, shows the Lesser Antilles of today to have been submarine volcanoes through the early Miocene (fig. 3, p. 728), but he makes no reference to when they appeared above the surface. In the region of the Greater Antillean islands of

Hispaniola and Puerto Rico there has been some land continuously since the Cretaceous.

How anoles colonize islands by overwater dispersal has never been observed, but it is not difficult to imagine. During the rainy season, and particularly following hurricanes, large mats of floating vegetation come north from the Orinoco, passing along the east coast of Trinidad. Occasionally, lizards and/or their eggs may take advantage of this transport system and journey into the sea. Most would perish. However, some of the rafts must come to rest on the beaches of the Lesser Antilles.

Reference to an Atlas of Surface Currents of the North Atlantic (Hydrographic Office, Washington, D. C.) shows a general northwesterly trend; but this is not absolute, and for short distances movement might be in any direction.

Although we lack useful fossils, precise dates for the age of the islands, and the exact direction in which currents moved potential colonists, we still feel that a careful analysis of the probable phylogenetic relationships of the island forms within their species groups provides a very likely hypothesis about the probable history of colonization routes. The value of such speculation has been stated by Wilson (1965): "Evolutionary hypotheses might never be definitive by the standards of experimental biology, but they are valuable if they are both falsifiable and heuristic. That is, to be valid they should make concrete predictions that are capable of being negated if the hypothesis is false; and they should point the way to deeper, more meaningful investigations if they are momentarily upheld."

The phylogenetic relationships of the two major species groups will be discussed independently. But first, it is worth stating, in some detail, rules for evaluating characters as indicators of phylogenetic relationship. We shall follow Hennig (1966), who presents a formalized, methodological approach. It is therefore necessary to define some of his terms.

Characters or character conditions from which transformation started in a monophyletic group are termed *plesiomorphous*, and the derived conditions *apomorphous*. The presence of plesiomorphous characters in different species is called *symplesiomorphy*, the presence of apomorphous characters *synapomorphy*—always with the assumption that the compared characters belong to the same transformation series. It follows that monophyly can be established only by synapomorphous characters.

It does not matter whether the synapomorphy (a′) is present identically in all species, or whether it is present in different derived conditions (a′, a″). "Recognition that species or species groups with common apomorphous characters form a monophyletic group rests on the assumption that these characters were taken over from a stem species that only they share in common, and which already possessed these characters prior to first cleavage" (Hennig, 1966, p. 90).

If it is a question of determining the relationships *between* different species groups, "then it is of primary importance to show that each group has apomorphous characters, characters that are present only in it" (op. cit., p. 90).

Hennig feels that the concepts of symplesiomorphy and synapomorphy go beyond the range of what we ordinarily call homologous characters. "We started from the idea that a, a′, a″ are different characters in a transformation series. We can speak without reservation of homologous characters if a, a′, a″ are transformation stages of an organ. But the transformation a-a′-a″ may also consist in complete reduction of the organ. For example, the absence of the wings in fleas is undoubtedly an apomorphous character in comparison with the presence of wings in other holometabolic insects. On the other hand, the possession of wings is an apomorphous character in comparison to their absence in the so-called 'Apterygota.' In general we speak only of the homology of organs,

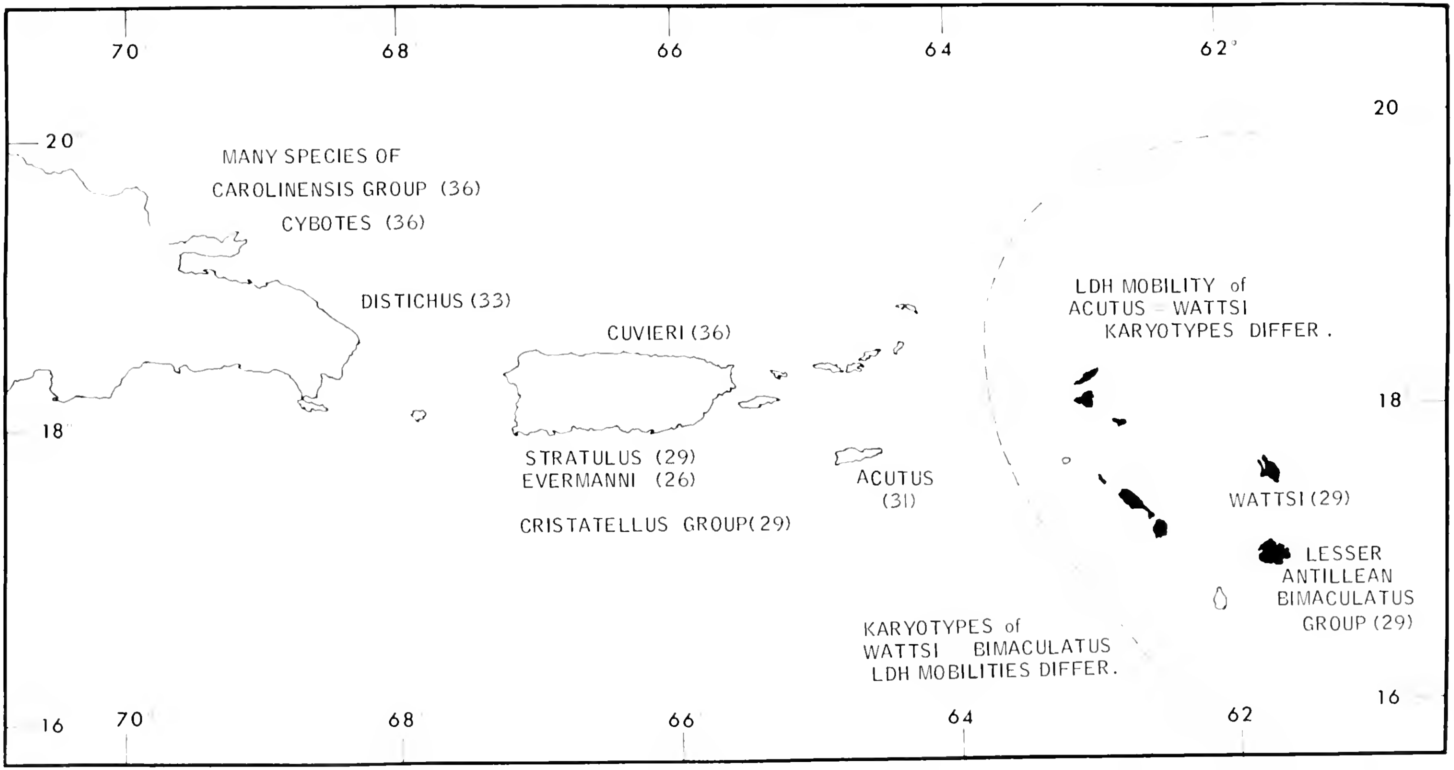


Figure 11. Distributional and karyotypic data for anoles of the *acutus*, *wattsi*, Puerto Rican, and Hispaniolan species groups. Numbers in parentheses are male diploid numbers. Islands shown in black are inhabited by *wattsi*. Dotted line separates the *wattsi* and *bimaculatus* group (to the east) from the *acutus* and Greater Antillean groups (to the west). *A. cybotes* of Hispaniola is considered a member of the predominantly Puerto Rican *cristatellus* group on the basis of osteology (Etheridge, 1960). Chromosome data were presented in Gorman and Atkins (1966). Chromosome data for the western Caribbean *carolinensis* species group were presented in Gorman, Atkins, and Holzinger (1967).

but a 'character' may also be the absence of an organ."

The *roquet* species group

By all standard museum techniques, the eight forms in this group are extremely closely related. Etheridge (1960) did not mention any skeletal differences among the forms that comprise this group. In fact, the *roquet* group, along with one other species (*agassizi*), forms a subgroup within the *latifrons* series distinguished by the presence of functional autotomic caudal vertebrae (a presumably primitive character widespread in other lizards and secondarily lost in the mainland alpha anoles). Underwood (1959) did not discuss any major differences in scutellation among the members of the *roquet* group.

Does the group meet the test of monophyly using Hennig's criteria? The LDH is characterized by very slow electrophoretic mobility in alkaline buffer. This differs from every other *Anolis* so far studied, including *frenatus*, a mainland member of the *latifrons* series (Gorman and Dessauer, 1966). The territorial display of all members of the group is characterized by the dewlap being held extended for long periods of time, as opposed to the dewlap pumping of most other *Anolis*. It would appear that these behavioral and biochemical characters are synapomorphous and indicate monophyly.

The karyotype of 2n=36 is common to many alpha *Anolis* and thus is plesiomorphous. Three members of the *roquet* group (*roquet*, *aeneus*, *extremus*) have the reduced chromosome number 2n=34. This is the derived condition and most likely occurred only once.

Therefore, if we are to find one member of the species group that might be the most primitive, we will have to choose from the 2n=36 group. Two of these five forms, *richardi* and *griseus*, are giant anoles. This appears to be a specialized condition that evolved under sympatry, under selective pressure for splitting the food niche.

Of the three remaining candidates (*luciae*, *bonairensis*, and *trinitatis*), *luciae* appears best to fill the requirements of a probable ancestor of the group. It is intermediate in size between the two giants and the other forms. St. Lucia, while not quite in the center of distribution of the species group, is somewhat centrally located—for there are *roquet* group members on islands to the southeast (Barbados), southwest (Bonaire), due north (Martinique), and due south (Grenada bank and St. Vincent).

Moreover, evidence from territorial display behavior supports the hypothesis of primitiveness for *luciae*. It will be recalled that members of the *roquet* group are characterized by not pumping the dewlap and that this appears to be the derived condition. In display, *luciae* bobs multiple series in a long head-bobbing sequence. As each series ends, there is a pause and an extremely slight dewlap retraction, then re-extension as a second series begins. This may well be a vestige of dewlap pumping (Gorman, 1968).

Is it likely that St. Lucia and not an island nearer to the South American mainland, such as Grenada or St. Vincent, would be first colonized? In point of fact, we know little about actual patterns of colonization of the islands. However, two genera of snakes, *Bothrops* and *Constrictor*, are known from St. Lucia and islands to the north, but not from St. Vincent or Grenada (Lazell, 1964b). It is possible that they have never reached the latter islands. The distance between St. Lucia and the nearest points on the mainland is not a great one for anoles to cross (approximately 200 miles); Williams (manuscript) has shown that *A. allisoni* has colonized the Islas de la Bahia from Cuba, travelling a distance of some 400 miles. Other iguanids have crossed from the South American mainland to the Galapagos, a distance of 600 miles.

If, in fact, the original colonists came on debris from the Orinoco, and they were swept slightly east out to sea as the currents

were moving north, the difference in distance from the mainland to Grenada or St. Lucia becomes negligible.

Let us accept for the moment the hypothesis that *luciae* is the most primitive member of the group and, in fact, that St. Lucia represents the ancestral home of the *roquet* group, and try to follow the sequence of colonizations (=phylogeny). We shall discuss possible alternatives later.

We infer that St. Vincent was twice colonized from St. Lucia; the second colonization took place after the first colonists had differentiated from the St. Lucia stock. There thus were two species on St. Vincent and, with two species sympatric, we might expect selection for size and habitat preference to reduce competition for food and to eliminate wastage of gametes in unsuccessful interspecific matings.

In fact, this model picture is precisely borne out by the anoles on St. Vincent. We find there *griseus*, a giant anole found primarily high in trees in deep shade, and *trinitatis*, a smaller species (and smaller than *luciae*) that occupies more open sites. Both retain the ancestral karyotype and LDH. In display behavior, *griseus* remains extremely close to *luciae;* the display of *trinitatis* is somewhat more modified.

The consistent color difference between the two species (*trinitatis* is green and unmottled; *griseus* is grey-brown and patterned) may have been fixed by selection as another recognition signal, in addition to size and habitat differences.

Next, we postulate that the giant *griseus* reached the Grenada bank, where it evolved into *richardi*. These two forms are very closely related on externals and, in fact, we know of no diagnosis that will separate them unequivocally. They were considered conspecific on the basis of blood proteins, which were very similar, including a common hemoglobin. The only difference found was in transferrin, a protein that appears to be evolutionarily labile in the Reptilia (Gorman and Dessauer, 1966). Now, however, we have found an LDH difference. Because *richardi's* LDH differs from that of the other seven members of the species group, and since *richardi* is also a specialized form (giant) with a display less like that of *luciae* than is the display of *griseus*, it is logical to consider the LDH of *richardi* the derived (apomorphous) condition. The *richardi* of Tobago hardly differs from that of the Grenada bank, and recent colonization of this continental island from the Grenada bank is assumed.

The derivation of *A. bonairensis* is not clear. But it is possible that it, too, is derived from *A. luciae*. Bonaire lies far to the west of the main Lesser Antillean chain. However, *A. bonairensis* is certainly a member of the *roquet* species group, sharing common osteological (Etheridge, 1960), behavioral (Gorman, 1968), biochemical (Gorman and Dessauer, 1966), and cytological (Gorman and Atkins, 1967) characters. It is clearly within the species group in terms of blood proteins, but we could not place it particularly close to any one form. When the species was described (Ruthven, 1923), it was compared with *roquet* and *aeneus*. However, in chromosomes it falls within the primitive group and could hardly have been derived from *aeneus*. In display behavior it has unique species-specific components which seem, however, to be most similar to those of *luciae*.

Hummelinck (1940) described a subspecies of *bonairensis* called *blanquillanus* from the island of La Blanquilla (see Fig. 2), which lies approximately halfway between Grenada and Bonaire. Unfortunately, live lizards of this form have been unavailable for study. It is probable that *blanquillanus* is the living intermediate between *luciae* and *bonairensis*.

J. D. Lazell, Jr., who is studying the external morphology of Lesser Antillean anoles, informs us (personal communication) that in several characters *bonairensis* is most closely allied with *luciae*.

What then of the three forms with the reduced chromosome number? These three,

aeneus, extremus, and *roquet,* are very closely related, *inter se,* and have at times been considered conspecific (Underwood, 1959). Gorman and Dessauer (1965) showed that in terms of transferrins and hemoglobins the three form a linear series with *extremus* in the center. That is, *extremus* shares a common hemoglobin with *roquet,* and a common transferrin pattern with *aeneus,* while *roquet* and *aeneus* differ from each other in both these proteins.

The probable ancestor of this subgroup is *A. trinitatis.* On the basis of externals (other than color) it is only with great difficulty that one can distinguish *trinitatis* from *aeneus.* However, *trinitatis* differs from the subgroup in hemoglobin and transferrin (Gorman and Dessauer, 1966), display (Gorman, 1968), and by a pair of microchromosomes (Gorman and Atkins, 1967). The karyotypic difference, we now know, is even more profound. Studies of meiosis in *trinitatis-aeneus* hybrid males (Gorman and Atkins, 1968b) show an arrest at metaphase I, with poor pairing ability of the macrochromosomes; i.e., there are numerous univalents.

Colonization may have gone in one of two likely ways. Either from St. Vincent to Grenada, where chromosome loss occurred leading to *aeneus* (this loss of a chromosome pair could be interpreted as having been selected for as an additional isolating mechanism between the giant and the small species); or from St. Vincent to Barbados where chromosome loss was accidental but became established. If the former were the case, then the route of colonization would have been Grenada to Barbados to Martinique, whereas if Barbados were first colonized, there would have been a colonization in two directions, to Grenada and Martinique. It is fruitless to argue this further with our present state of knowledge.

Figures 12 and 13 summarize the possible colonization routes taken by the *roquet* group, as outlined above. A very important point in this hypothesis, and one that we shall return to later, is that Martinique was the most recently colonized in the main chain.

The hypothesis of zoogeographic movements in this species group is based entirely upon the analysis of the phylogeny of the group. This produces a complex pattern of distribution. However, no simple model will suffice. Darlington (1957, p. 485) proposes two models to explain island patterns of distribution. One is termed the *immigrant pattern.* "Distance is basically important. Unless other factors are very unequal, animals dispersing from a continent to an archipelago may usually be expected to reach nearest islands first and to spread to other islands across the narrowest water gaps. The resulting pattern of distribution *should be orderly* [italics ours], with related forms occurring in series on adjacent islands along the route of immigration." This model is clearly not directly applicable to our system. For we would then expect that the island nearest the mainland (Grenada) would have anoles closest to the mainland stock—but, in fact, the two Grenada bank forms, *aeneus* and *richardi,* both have important apomorphous characters: *richardi* the derived LDH, and *aeneus* the derived karyotype.

Darlington's second model, to explain the *relict pattern,* is not at all applicable to the *roquet* group. "If a group of animals were once well represented on an archipelago and were then reduced in numbers and eliminated on some of the islands. . . . the survivors would probably not form an orderly series on adjacent islands but would occur irregularly" (op. cit. p. 485). There is absolutely no evidence that leads us to believe that any anoles are relicts in the Lesser Antilles.

However, the model of movements that we propose does not really differ too much from Darlington's immigrant pattern, *if St. Lucia and not Grenada was the first colonized island.* Then, most subsequent colonizations are hops to the nearest adjacent islands; from St. Lucia to St. Vincent twice, from St. Vincent to the Grenada bank twice,

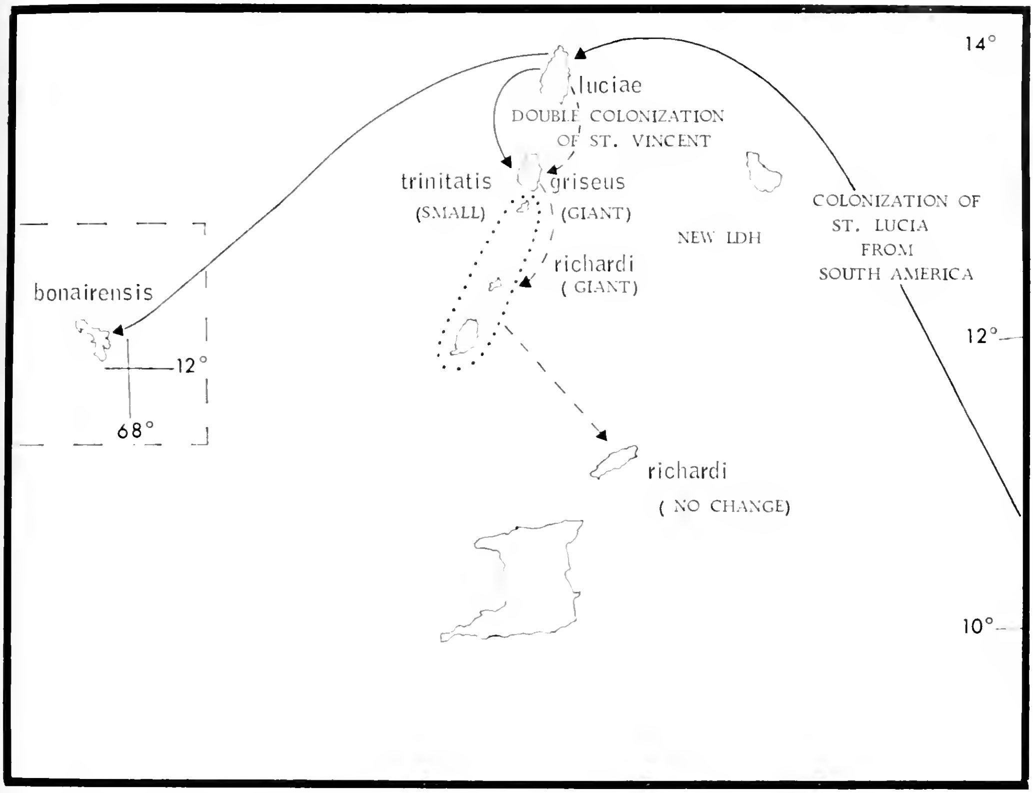


Figure 12. Possible colonization routes of the *roquet* group. Colonization of St. Lucia from South America and radiation from St. Lucia of the five forms with the primitive karyotype 2n = 36. Broken arrows trace the path of the giant forms, solid arrows the small forms.

from the Grenada bank to Barbados, and from Barbados to the nearest available "empty" island, Martinique. Let us re-emphasize that the differences in distance from the Orinoco to St. Lucia and to Grenada are actually fairly negligible compared with the over-water colonizing ability already established for *Anolis*.

Furthermore, any hypothesis involving replacement or successive waves of colonization requires several long-distance over-water successful journeys. Yet, as Darlington states, "the death rate of most terrestrial animals during dispersal across salt water is presumably high and presumably forms a geometric progression: if only one individual in a thousand survives the crossing of a hundred miles of sea, only one in a thousand of the remainder will be expected to survive the second hundred miles" (op. cit., p. 485). We would argue that the probability of successful colonization between adjacent island banks is much greater than the probability of multiple colonizations from the mainland, even though the proposed inter-island colonization may go against prevailing currents. Recall that over short distances, current movement may be in any direction.

There is a further factor that argues against multiple mainland colonization. Members of the *roquet* group are extremely closely related *inter se;* yet they are not very close to any living mainland forms. We would have to postulate extinction of an ancestor that was doing rather well and

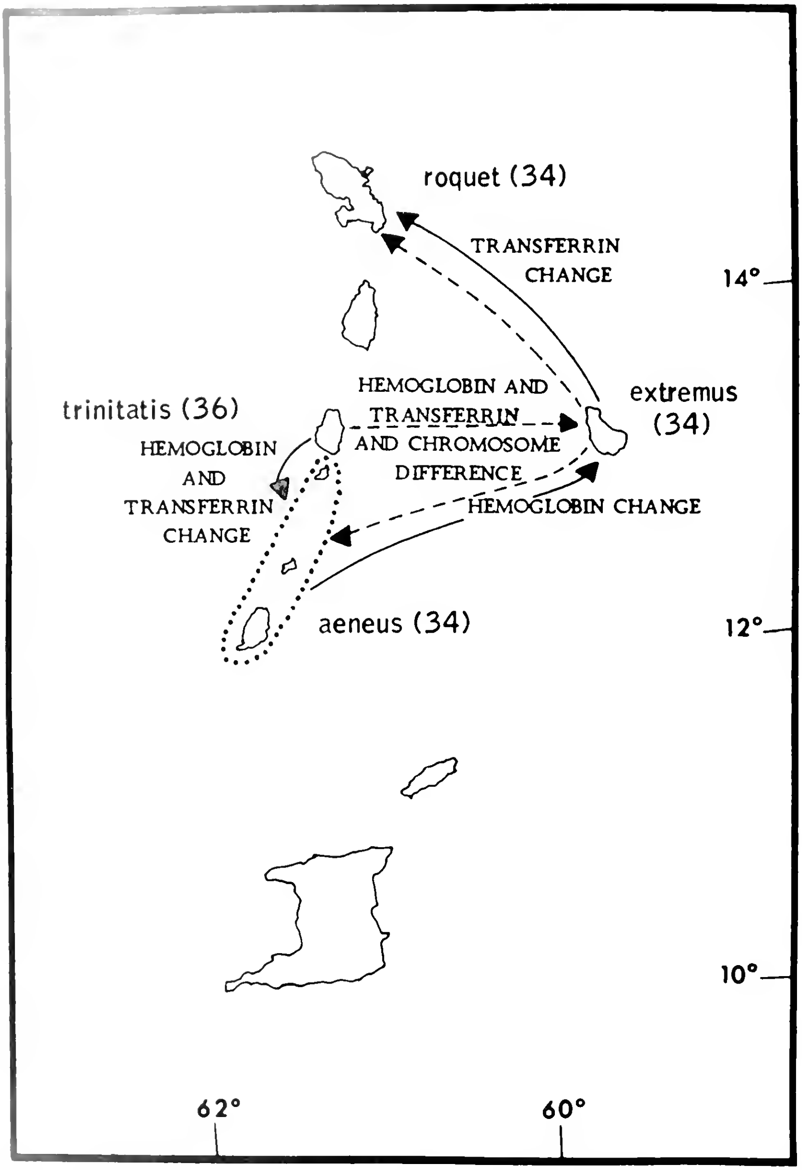


Figure 13. Possible colonization routes of the *roquet* group; the origin and dispersal routes of the advanced 2n = 34 subgroup. Two possible pathways are illustrated. Both originate from St. Vincent where *trinitatis* 2n = 36. Solid arrows show colonization to the Grenada bank, then to Barbados and then Martinique. Broken arrows show colonization from St. Vincent to Barbados and double colonization from Barbados to Grenada and Martinique.

sending out numerous colonists. There is no obvious reason why *roquet* group anoles would not do well on the mainland and, in fact, *aeneus* which has been introduced onto Trinidad and Guayana (present patterns of distribution could only be accounted for by introduction), is flourishing and possibly spreading. The simplest

model, then, is to consider the *roquet* group autochthonous to the Lesser Antilles.

The most difficult part of the *roquet* distribution to understand is the presence of *bonairensis* far to the west. To derive this species from *luciae* we must invoke long distance migration to the south (against prevailing currents) and west (with prevailing currents). An alternative might be via Blanquilla, and colonization of Blanquilla may have been from St. Vincent or, possibly, from Grenada *before* the establishment of chromosome loss in what ultimately became *aeneus* (see Fig. 12).

The *bimaculatus* species group

To understand the broad features of the Lesser Antillean *bimaculatus* forms, we must first examine the Puerto Rican situation. There, two species (*cuvieri* and *occultus*) have the primitive alpha anole karyotype characterized by six pairs of metacentric macrochromosomes, a sharp break between macro- and microchromosomes, and no obvious sex chromosomal heteromorphism. This appears quite unrelated to the karyotype of the *bimaculatus* group *sensu stricto*, which has complex sex chromosomal heteromorphism, an increased number of autosomal macrochromosomes, some of which are acrocentric or subacrocentric, and a correspondingly reduced break between the size of the smallest macrochromosomes and the microchromosomes.

While we do not have enough living intermediates to trace every part of the origin of the Lesser Antillean *bimaculatus* karyotype, the *acutus* group provides valuable clues. All members of this group have karyotypes that in some way resemble typical alpha *Anolis* (primitive) and Lesser Antillean *bimaculatus* (highly derived). In three species, *acutus*, *stratulus*, and *evermanni*, the six largest pairs of chromosomes are metacentric, and there tends to be a fairly sharp break between pairs six and seven, as in most alpha *Anolis*. But all members of the *acutus* group have diploid numbers reduced from the primitive 36, and all but *evermanni* have an X_1X_2Y sex chromosomal mechanism. In these respects they resemble the Lesser Antillean *bimaculatus* forms.

Anolis distichus is unusual in the *acutus* series because the sharp break in chromosomes occurs between pairs five and six, instead of between six and seven. This is probably a derived condition resulting from additional translocations and rearrangements following the establishment of the *acutus*-like karyotype.

There is a similarity between the chromosomes of the *acutus* group and the beta anoles (see Gorman and Atkins, 1966, for figures). This is interpreted as convergence in the evolution of the karyotype. In both groups there is an increase in the number of metacentric macrochromosomes, seemingly at the expense of the microchromosomes.

What appears likely, then, is rapid evolution of the anole fauna on the Puerto Rico bank from a primitive alpha stock. This led to a group characterized by a reduced diploid number and a sex trivalent. Two groups emerged from this line, the *cristatellus* group and the *acutus* group. The two are karyotypically very similar, and on the basis of chromosomes alone, we would not have separated them. The most divergent member of the *acutus* group is *evermanni*, with its low chromosome number (the lowest known in the genus), rapid LDH mobility, and a heteromorphic pair of sex chromosomes rather than the three sex chromosomes. The *evermanni* stock probably diverged early and secondarily lost the X_1X_2Y sex chromosomal system.

It is significant that the LDHs of *wattsi*, *acutus*, and Hispaniolan *distichus* appear identical[1] whereas in chromosomes, *wattsi* and the Lesser Antillean *bimaculatus* group are similar. *A. wattsi* has traditionally been considered taxonomically close to *acutus* (e.g. Underwood, 1962: 70), and the LDH

[1] Identical electrophoretic mobility is suggestive of, but does not prove, structural identity of proteins.

finding corroborates morphological studies. The stock directly ancestral to *distichus* and *acutus* probably later underwent additional centric fusions and inversions leading to the *wattsi* karyotype; this stock in turn gave rise to the Lesser Antillean *bimaculatus* group, which evolved a new LDH that has remained constant in all races of the species group. These facts argue again for a single successful colonist in the northern Lesser Antilles which, through more or less stepwise colonization, filled the northern half of this chain, much as the *roquet* group in the south evolved by stepwise colonization, radiating from St. Lucia.

The similarity in LDH mobility of Hispaniolan *distichus* and *acutus*, the two species in the *acutus* group with the highest chromosome number, implies that this LDH may be primitive for the *acutus* subgroup. The peripheral Bahaman populations would have an apomorphous LDH, as would the Puerto Rican species *stratulus* and *evermanni*.

The four members of the *acutus* group have four distinct karyotypes and at least four different LDHs (there being interisland variation in *distichus*). The peripherally evolved Lesser Antillean *bimaculatus* group, although representing eight distinct forms (a ninth, *A. nubilus* from Redonda, was unavailable for study), has only one LDH and only two karyotypes. Note that in the *roquet* group, in which eight distinct forms were also studied, there are only two different LDHs and two different karyotypes. This may represent a canalization of certain characters in peripherally isolated populations when compared with the species-rich source area.

Because detailed behavioral and biochemical studies have not been undertaken for the Lesser Antillean *bimaculatus* group, we are unable to provide directional arrows based on the sort of evidence used for the *roquet* group. However, it appears clear that the primitive members of the group are in the northern and western parts of the range. In chromosomal characters, the *acutus* group is intermediate between primitive alpha and *wattsi*. *A. wattsi*, in turn, shares an important character with *acutus* (LDH) and with Lesser Antillean *bimaculatus* (chromosomes). Thus the most highly derived forms, the *bimaculatus* group *sensu stricto*, are found at the extreme south and east of the range of the group.

If we assume that the colonization followed the simple immigrant pattern of Darlington, we would expect that the most primitive members of the series would be in the northwest (they are) and that colonization occurred in an almost stepwise manner south and east along the chain. Because this is against major currents, we would not expect any long distance "leap-frogging." But again, distances between islands are so small that short hops south could certainly occur. Thus it is not improbable that Dominica, the southernmost of the *bimaculatus* islands, was the last colonized, much as Martinique, the northernmost of the *roquet* islands, was probably the last colonized by that group.

This raises a discussion of karyotypic comparison of Dominica *oculatus* with other members of the *bimaculatus* group. Earlier, it was pointed out that the difference in karyotype was Robertsonian. The number of chromosomal arms is the same in *oculatus* and in the other members of the species group (see Figs. 7A, B). However, two pairs of acrocentric chromosomes in *oculatus* are represented by a single pair of metacentric chromosomes in all the other members of the species group.

Was there an increase in chromosome number by centric fission? The answer is probably yes. Centric fusions (reducing the diploid number) appear to be much more common than the reverse process (White, 1963), and centric fusion, or complete loss, is the mechanism that we postulate in the *roquet* group, in which three forms have the reduced chromosome number. Centric fission, however, has been substantiated in the Iguanidae (*Plica plica*, see Gorman, Atkins, and Holzinger, 1967). Why

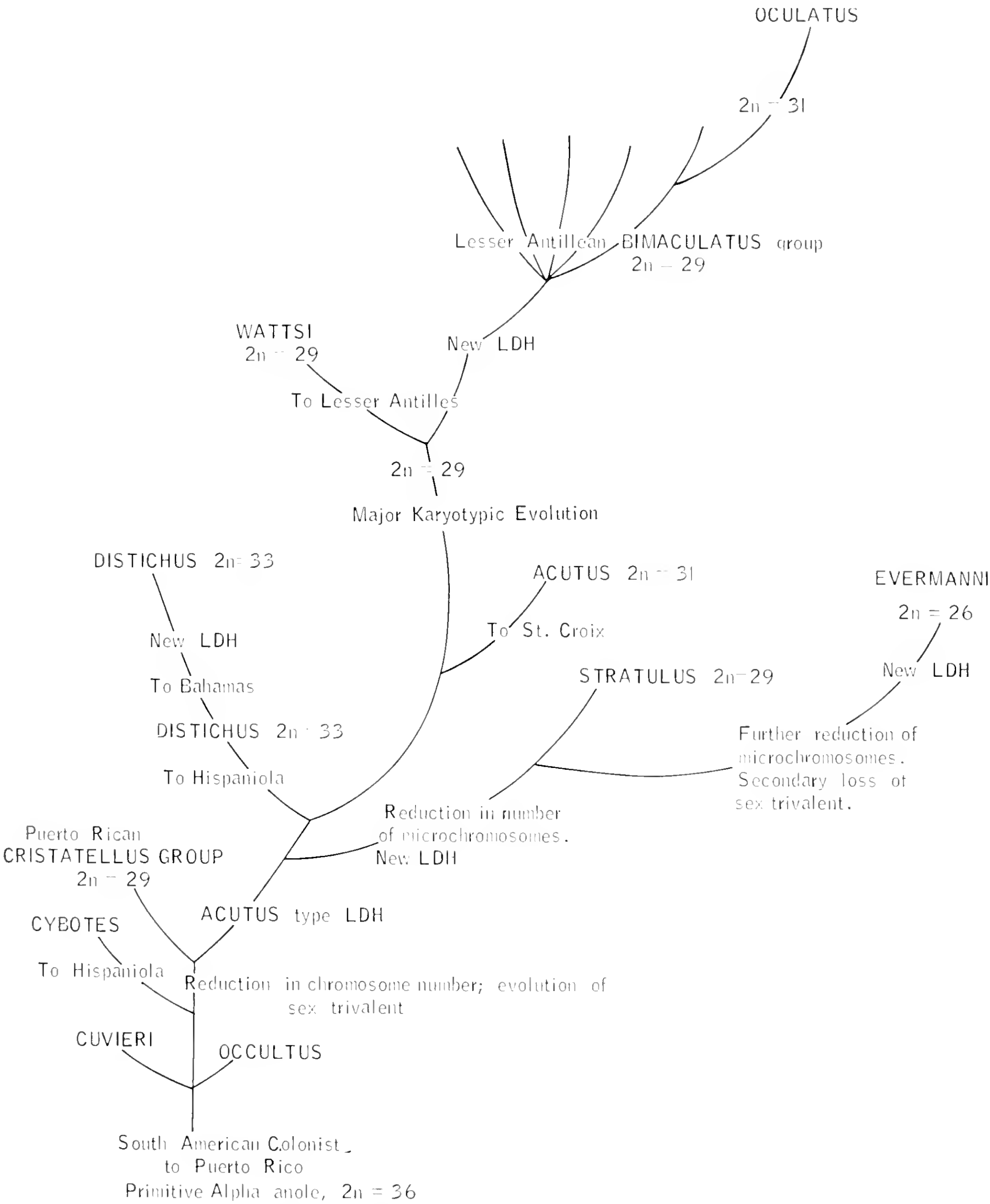


Figure 14. Proposed phylogeny of the *bimaculatus*, *acutus*, and Puerto Rican species groups of *Anolis*. Major changes in karyotype, LDH, and geographic movements are indicated.

is it invoked in this case? Acrocentric autosomes are unknown in any other alpha *Anolis*. The karyotype thus appears one step more derived than the karyotypes of the other Lesser Antillean members of the *bimaculatus* series.

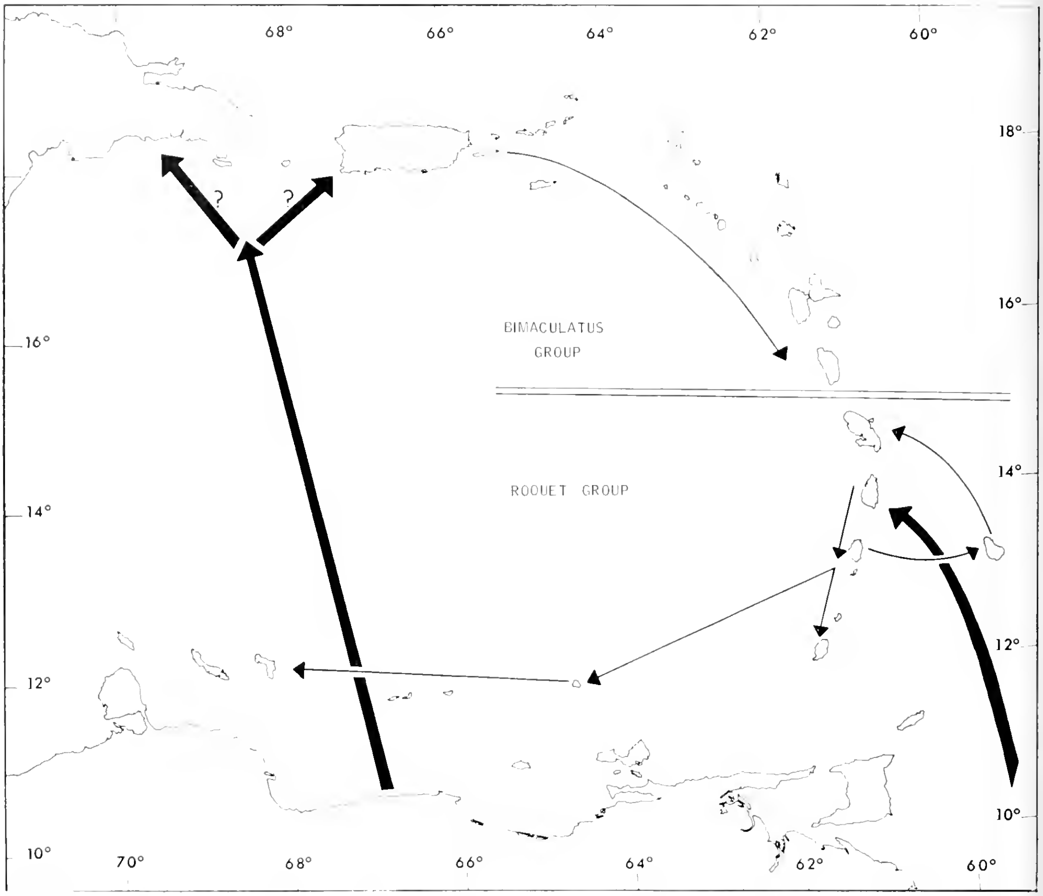


Figure 15. Summary of the general patterns of biogeographic movements. Heavy arrows indicate colonization from South America (they are not meant to imply exact paths). Two major movements are postulated. One is to the Greater Antilles, with subsequent colonization of the northern Lesser Antilles. This gave rise to the *bimaculatus* group. The second is to the southern Lesser Antilles, where the *roquet* group evolved. Light arrows indicate general movements within the species groups, as discussed in the text. The double horizontal line indicates the geographic break between the two Lesser Antillean species groups.

Utilizing the data from chromosomes and LDH, we can propose a model of the probable phylogenetic history of the Puerto Rican and northern Lesser Antillean anoles (Fig. 14).

There is only one inconsistency between this model and Etheridge's classification of anoles. Puerto Rican members of the *cristatellus* group have a derived karyotype. The common Hispaniolan species *A. cybotes* has the primitive alpha karyotype (2n=36) with the absence of sex chromosomal heteromorphism (Gorman and Atkins, 1966). Yet Etheridge (1960) places this species in the *cristatellus* group on the basis of osteology. It shares with the other members of this group not only the same osteological formulas (such as number of attached and free parasternals), but also an osteological character almost unique to the group—"jaw sculpturing" (one or more deep semilunar excavations on the lower surface of the dentary in adult males). If we are to reconcile this conflict, we could assume

that a proto-*cristatellus* stock colonized Hispaniola from Puerto Rico before the commencement of the reconstruction of the karyotype. Perhaps this stock had a tendency to evolve "jaw sculpturing," and the character arose in parallel in the two island populations. Or possibly, the character is convergent: there is one non-*cristatellus* group member (*A. argillaceus* of the *angusticeps* series) that has independently arrived at a similar condition (Etheridge, 1960, p. 74).

One final point needs discussion—the mutual geographic exclusion of the two Lesser Antillean species groups. Underwood (1959) wrote, "There is every reason to believe that anoles disperse readily; I am therefore at a loss to explain why the two groups do not overlap." It is clear, however, that one or two species of *Anolis* can easily saturate a Lesser Antillean island. The short distances between the islands must make it possible for waifs to cross from time to time. Yet each island bank has distinct forms. Once an empty island receives successful colonists, it probably takes a relatively short time for a nearly complete occupation of the generalized anole niche. Thus a new arrival to an island already colonized will suffer from the competition of numerous healthy, well-adapted congeners. The probability of successful establishment is thus much less than on a comparable island devoid of anoles.

In all cases in the Lesser Antilles where two species of anoles are sympatric, they differ greatly in size (*wattsi* is very small and is sympatric with several members of the *bimaculatus* group, including the two largest forms; *richardi* and *griseus* are very large and are sympatric with the two smallest *roquet* group anoles). There are also differences in habitat preference (Schoener and Gorman, 1968).

The Lesser Antilles were probably colonized at more or less the same time from two separate directions. The *roquet* group, derived from South America, filled the southern islands, while *bimaculatus*, starting on the Puerto Rican bank, filled the northern islands. Somewhat fortuitously, the northernmost of the *roquet* group islands and the southernmost of the *bimaculatus* group islands were the last to be colonized by anoles. These islands were then filled up by moderate sized lizards of broad ecological adaptability, and the two groups were unable to establish themselves on islands already held. Figure 15 summarizes the biogeographic movements discussed.

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The Subfamily Tellininae in South African Waters (Bivalvia, Mollusca)

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THE SUBFAMILY TELLININAE IN SOUTH AFRICAN WATERS (BIVALVIA, MOLLUSCA)

KENNETH J. BOSS

CONTENTS

INTRODUCTION

The family Tellinidae is a widely distributed, entirely marine, eulamellibranch group of bivalves with three subfamilial elements—the Tellininae, the Macominae and the Strigillinae. With its phylogenetic roots in the Mesozoic, the family had already undergone considerable radiation by the Upper Cretaceous, and by the base of the Neogene, the lineages culminating in the Recent representatives had been established. The Tellininae is a rather conspicuous member of the tropical and subtropical infaunal benthos, whereas the Macominae, possibly less highly speciated, has its stronghold in the cold temperate, boreal, and arctic realms.

The Strigillinae, rounded in shape, sculptured with scissulations, and usually highly colored, is also tropical and subtropical in its distribution and richest in number of species in the eastern Pacific-Caribbean region (Boss, 1969).

Having been for some time interested in the systematics of the genus *Tellina* (Boss 1966b), I began studying the species of South African waters while working on board the R/V ANTON BRUUN during Cruise 7 of the International Indian Ocean Expedition off the coast of southeast Africa.

The species taken in South Africa bear considerable resemblance to those of the western Atlantic-eastern Pacific as well as the Mediterranean areas. Thus my interest in the evolution of this group and in the interrelationships of the faunas expanded into the present review of the South African species. Any geographically restricted study of widely dispersed organisms in the marine habitat is necessarily incomplete, since not all the species—either fossil or Recent—can be taken into consideration, and since the interpretation of the differentiation of the group can be, at best, only an approximation of what has actually happened.

When one studies the species-complexes of the South African area that are in

reality of Indo-Pacific distribution, one fact becomes immediately apparent: most species live throughout the Indo-Pacific from east African waters to as far south as Durban and as far east as the Hawaiian Islands. These species have been subject to overnaming. Species such as *Tellina semen*, *T. capsoides*, and *T. perna* have extensive synonymies, which will no doubt be increased as more of the obscure, named forms of the Philippines, Indonesia, and India are recognized for what they really are.

The major papers dealing with the taxonomy of the Tellinidae have recently been discussed (Boss, 1966b). The genus *Tellina* was established by Linnaeus (1758), and the species that he originally included have been reviewed by Hanley (1855), Römer (1871), and Dodge (1952). Monographic revisions or surveys of the family began with Spengler (1798), though Schröter (1788) discussed numerous species, and were continued in the 19th century with the work of Hanley (1846), Sowerby (1869), Römer (1870–73), and Bertin (1878). Dall (1900) treated the superspecific taxa; Salisbury (1934) listed the superspecific groups and renamed a number of homonyms; and Afshar (1950) attempted a revision of the generic and infrageneric taxa.

Barnard (1958) presented an historical résumé of the workers who have described South African mollusks. With regard to the tellens, Krauss (1848) was among the earliest malacologists to publish specifically on the South African fauna. Later, von Martens (1874) reported on specimens collected by Fritsch. In a series of papers, Sowerby (1889a and b; 1892; 1894; 1897; 1904) described many new species, including some collected by the trawler PIETER FAURE; Tomlin (1926) also worked on some of that material. The collection made by Turton was reported on by Bartsch (1915) and later by Turton himself (1932). The latest and most important contribution to the knowledge of the South African malacofauna is the work of Barnard (1964b). Boshoff (1965) discussed the bivalves of Inhaca Island, Mozambique. The large national oceanographic expeditions usually rounded the Cape on their way home and collected in these waters. Smith (1885) did the CHALLENGER lamellibranchs and Thiele and Jaeckel (1931) worked up those of the VALDIVIA.

Recently an extensive paper on the superfamily Tellinacea in Chinese seas has been published by Skarlato (1965). He discusses 54 species of the family Tellinidae. Of these, more than half are referable to *Tellina* in its broadest sense. In general, what I have reduced to subgenera, Skarlato employs as genera. Of particular interest, however, is his excellently detailed geographic analysis and recognition of certain species that are widely distributed in the Indo-Pacific region.

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ABBREVIATIONS

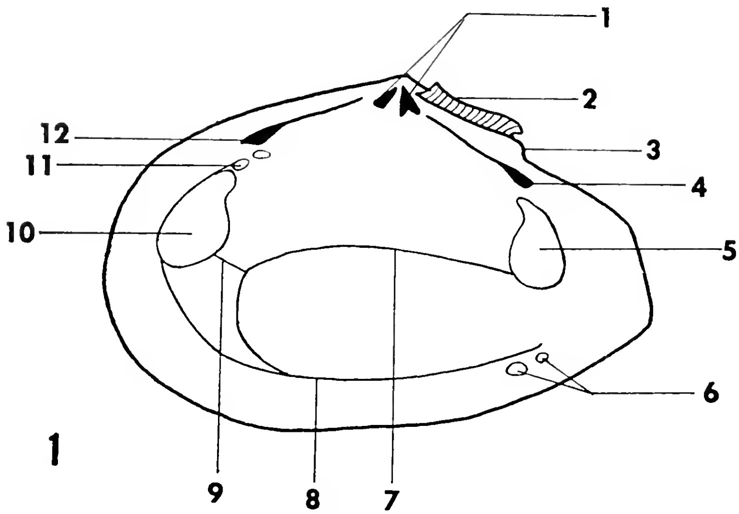
AMNH — American Museum of Natural History, New York.
ANSP — Academy of Natural Sciences of Philadelphia, Pennsylvania.
BMNH — British Museum (Natural History).
DM — Durban Museum, Durban.
MCZ — Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.
MHNG — Muséum d'Histoire Naturelle, Geneva.
MNHNP — Muséum National d'Histoire Naturelle, Paris.
NM — Natal Museum, Pietermaritzburg.
SAM — South African Museum, Cape Town.
UCT — University of Cape Town, Ecology Survey.
USNM — United States National Museum, Washington, D. C.

TAXONOMIC CHARACTERS

The characteristics of the shell serve as the basis for the systematics of the family Tellinidae — all its genera and all its species. Certain of the more noticeable anatomical features of the animals are reflected in the structure of the shell — a fact which at least in part justifies the reliance of the system on shell morphology.

Plate I illustrates the major conchological traits of *Tellina.* The most important elements are the teeth, which are comprised of two portions: (1) a cardinal complex consisting in the right valve of an anterior, single, variously thickened cardinal tooth and of a posterior, variously thickened and skewed, bifid cardinal tooth, and in the left valve of an anterior bifid cardinal tooth and of a single posterior cardinal tooth; and (2) a lateral dental complex of variable development. Interlocking the valves medially, the cardinal complex is supported by a hinge plate and is virtually the same throughout the family or within related families of the superfamily Tellinacea (e.g., Semelidae). The cardinal complex offers little of diagnostic value at levels below the family, although in certain species the right posterior bifid tooth is protuberant and strongly skewed posteriorly.

The lateral teeth, on the other hand, have been employed as the basis for distinguishing the Tellininae (with lateral teeth) and the Macominae (without lateral teeth). These teeth are differentiated projections of the hinge line and serve to stabilize and interlock the two opposing valves. A complete complement of lateral teeth totals four — one anterior and one posterior (in each valve). Those of the left valve tend to be less strongly developed, and the right anterior lateral tends to be the most strongly developed. The relative distances from the cardinal complex at which the lateral elements are developed are important in the recognition of certain groups. Thus, in *Tellina sensu stricto* and *Tellinella*, the right anterior lateral tooth is distal to the cardinal complex, whereas in *Tellinides* and *Homalina* that anterior lateral is virtually incorpo-



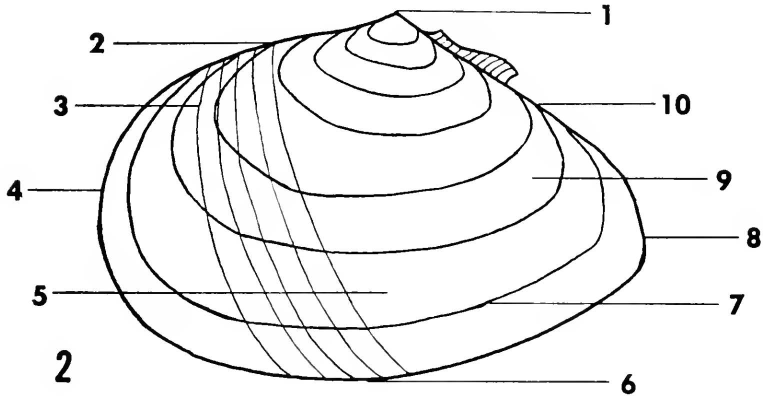


Plate 1. Diagrammatic representation of the shell morphology of a generalized *Tellina*. Fig. 1. Internal view of a right valve: 1, cardinal complex with the single, anterior, laminate cardinal tooth and the bifid, posterior cardinal tooth; 2, ligament; 3, nymphal callosity; 4, posterior lateral tooth; 5, posterior adductor muscle scar; 6, cruciform muscle scars; 7, pallial sinus; 8, pallial line; 9, interlinear scar; 10, anterior adductor scar; 11, pedal retractor scars; 12, anterior lateral tooth. Fig. 2. External view of a left valve: 1, umbo; 2, anterior dorsal margin; 3, oblique sulcus or scissulation; 4, anterior margin; 5, disc; 6, ventral margin; 7, concentric sculpture; 8, posterior margin; 9, posterior slope; 10, posterior dorsal margin.

rated into the cardinal complex, and in *Eurytellina* the tooth is proximal to it.

The ligament is opisthodetic (situated behind the umbos) and consists of an outer horny external sheath and a white internal calcareous element. The latter is supported by a thickening of the hinge line, which is called the nymphal callosity.

The ligament is usually short and protuberant, though in certain species it is elongate and thin (e.g., *Tellina* (*Phylloda*) *foliacea* Linnaeus) or tending to become internal (e.g., *Tellidora cristata* Recluz).

The external surface of the valves may be invested with variously developed sculpture, though the overwhelming majority of the species tend to be smooth or, at most, weakly and concentrically incised with fine sulcations. Acentric sulcations are found in the subfamilial Strigillinae and in a

number of subgenera (e.g., *Scissula*, *Fabulina*, *Scissulina*) (Boss 1966a). Raised and differentiated ridges or rasps are found in some species-complexes and groups (e.g., *T. scobinata* Linnaeus, *T. rastellum* Hanley, *T. palatam* Iredale).

Relatively strong concentric lirations are found in such groups as *Serratina*, *Tellinella*, and *Merisca*. Differentiated dorsal spines are usually extensions of sublamellate concentric sculptures (*Quadrans* and *Tellidora*). The lirations in *Cadella* and *Moerella* are closely spaced and rather smooth.

The internal surface of the valves shows many anatomical traits: the size and disposition of the anterior and posterior adductor muscles, the anterior and posterior pedal retractor muscles, and the ventral cruciform muscles. The pallial scars include those of the pallial sinus, impressed by the siphonal retractors, and the pallial line made by the muscles of the edge of the mantle. Infrequently an interlinear scar connects the pallial sinus with the anterior adductor muscle scar. The *Gestalt* of these muscle scars is usually specifically diagnostic — particularly when it is employed in conjunction with less easily described features, such as the outline of the valves, the truncation of the posterior end, or the thickness or color of the shell.

The shapes of all the muscles, though very similar in closely related species, may be very different in separate lineages. Thus in *T. liliana* Iredale from New Zealand, the anterior adductor is very long, narrow, and semilunate; in *T. palatam* Iredale of the Indo-Pacific, the posterior adductor muscle has an unusual ventral extension. The pallial sinus itself may be coextensive with the anterior adductor muscle in one valve only (e.g., *T. trilatera* Gmelin from South Africa) or in both valves (e.g., *T. punicea* Born of the western Atlantic). It may be coalescent with the pallial sinus for a short distance ventrally (*T. crassa* Pennant of the eastern Atlantic), or parallel to it for some time before becoming confluent (*T. capsoides* Lamarck of the Indo-Pacific), or completely coalescent (*T. madagascariensis* Gmelin of west Africa).

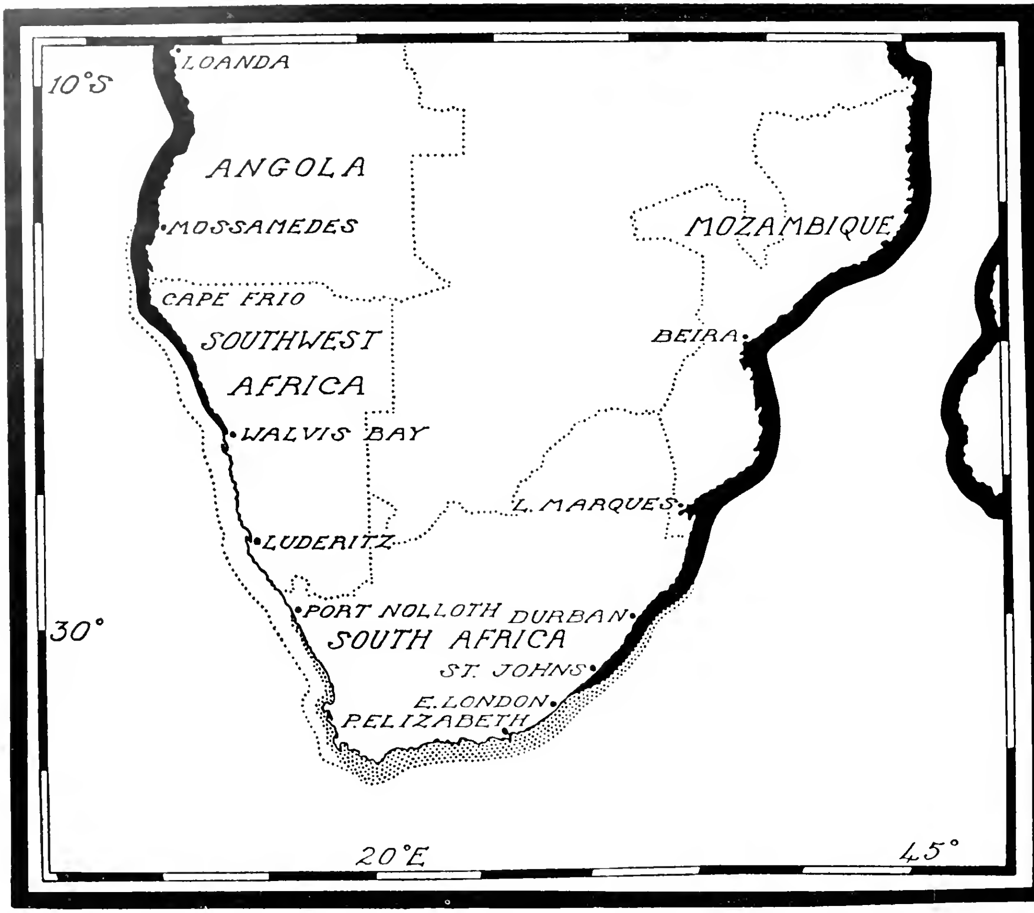
The cruciform muscle scars exhibit little variation and are characteristic of all the families of the Tellinacea. They are paired and may be subtended by colored rays or some differentiation of the shell (*T. opalina* Gmelin of the Indian Ocean and the East Indies). Usually the scars are rounded, but the right anterior one sometimes tends to be rectangular.

REMARKS ON ZOOGEOGRAPHY

The salient feature of the distribution of marine plants and animals in South Africa is the steady increase in the number of species from the west to the east coast. This species gradient was proposed by Gilchrist (1905) for offshore organisms and carefully documented for intertidal plants and animals by Stephenson (1947). Correlated with temperature, the gradient shows an increase in numbers of species of organisms from the cooler waters of the southwestern coast to the tropically influenced waters of Natal. Stephenson (1944) illustrated the decline in species numbers from Durban in the east to Port Nolloth in the west. Gilchrist also postulated that the number of individuals was greater in areas with a reduced number of species. The distribution of mollusks in South African waters was also discussed by von Martens (1903), Tomlin (1922), and Barnard (1958).

Three rather distinct faunal provinces were established for intertidal animals by Stephenson, and such faunal divisions are also recognizable for offshore organisms (see Map 1). Exhibiting a degree of overlap and, thereby, imperfectly circumscribed, these areas include:

1) A cold-water fauna along the west coast, extending from the Cape of Good Hope north to southwest Africa, where the tropical West African zone is encountered near Cape Frio, Angola. This element has been referred to as the Namaqua fauna.



Map 1. Southern Africa, showing the approximate distribution of its principal coastal faunas. The two tropical faunas are shown in black—the southern part of the tropical west African fauna on the left, southwestern termination of the Indo-Pacific fauna on the right. The 'Cape' fauna in the strictest sense, a warm-temperate fauna centering about the south coast of the Republic of South Africa, is stippled. The cold-water or Namaqua fauna of the southern part of the west coast is shown in white bounded by a dotted line. Overlap between these faunas is indicated (after Stephenson, 1947).

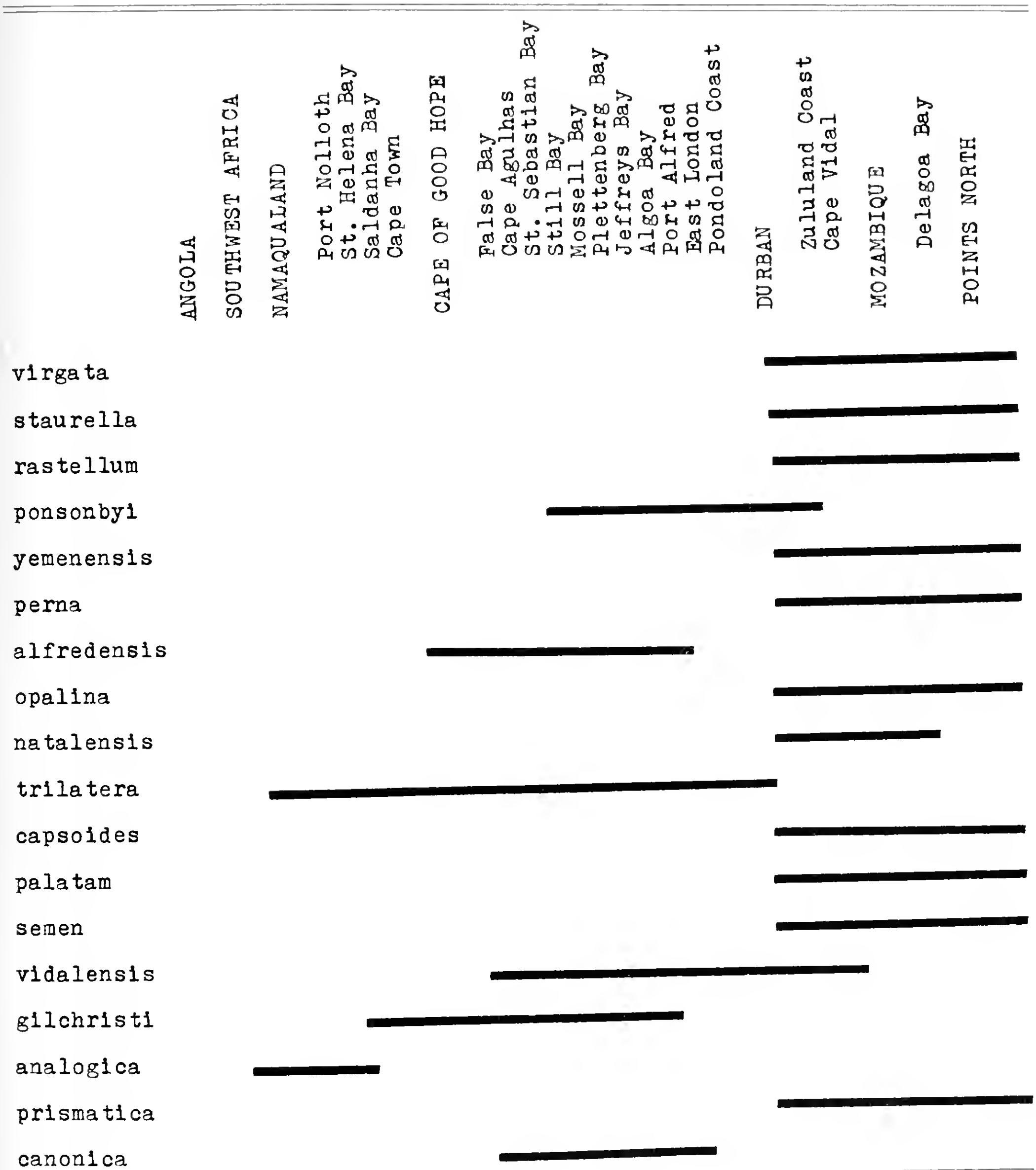
2) A southern, warm-temperate fauna between Port Elizabeth in the east and Cape Agulhas in the south.

3) A tropical and subtropical element from the Natal coast southward to East London.

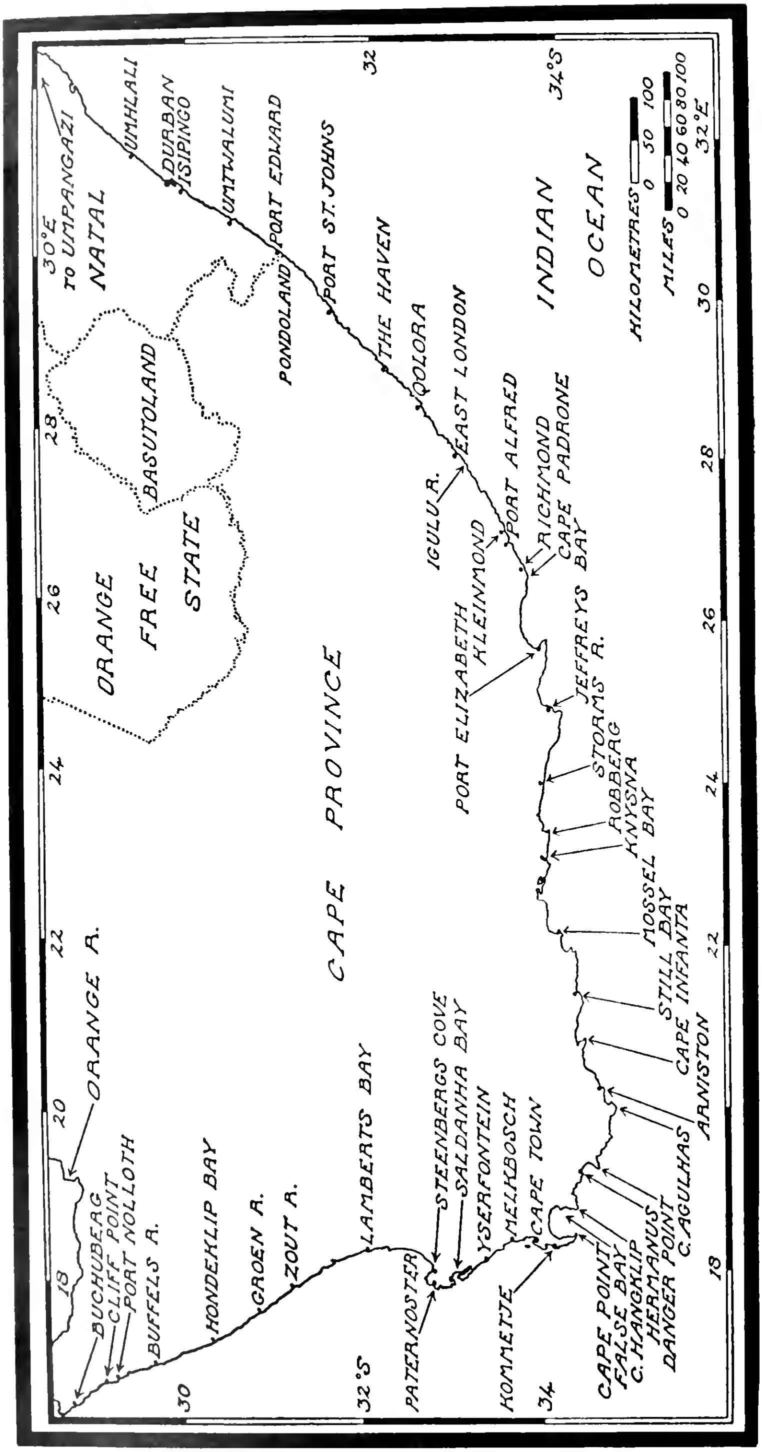
Although Stephenson's results and interpretations are based on an intensive study of intertidal organisms, his generalizations in regard to the three faunal elements apply in most respects to subtidal and offshore organisms. Species of *Tellina* are sublittoral or offshore infaunal animals that live in sandy, muddy, or gravelly substrates in predominantly tropical warm-temperate waters. Their distribution in South Africa, however, is similar to that of *Siphonaria*, an intertidal limpet-like pulmonate gastropod, which Allanson (1958) has recently discussed.

Table 1 gives the distribution of the species of South African *Tellina*, and Map 2 shows the main localities along the South African coast. The number of species in-

Table 1. The distribution of Tellininae along the coast of South Africa.



creases from west to east; this increase is related to the coastal water temperatures. The cold waters of the west coast are obviously a barrier to *Tellina.* A single species, *analogica,* is strictly western, whereas the other two that occur in that area, *gilchristi* and *trilatera,* have ranges that overlap the southern region and, in the case of *trilatera,* even the subtropical eastern area. Of the remaining species of South African *Tellina,* two have ranges entirely within the southern province: *alfredensis* and *canonica;* three occur in the south but overlap into the subtropical



Map 2. Principal localities along the coast of the Republic of South Africa (after Stephenson, 1944).

area near Durban: *ponsonbyi*, *trilatera*, and *vidalensis*. Eleven species are eastern forms, with distributions that usually range into the tropical Indo-Pacific. Species such as *virgata*, *staurella*, *rastellum*, *perna*, *opalina*, *capsoides*, *palatam*, and *semen* are extensively distributed throughout the Indian and Pacific Oceans.

Species apparently endemic to South Africa include: *ponsonbyi*, *alfredensis*, *canonica*, *analogica*, *trilatera*, *gilchristi*, and *vidalensis*. Of these, the relatively well-known and more conspicuous species exhibit interesting relationships to species in other parts of the world. They are not closely related to the western Atlantic-eastern Pacific species or to those complexes of the European north Atlantic and Mediterranean groups, but rather to those isolated in regions of South Australia and New Zealand. In the case of *ponsonbyi*, its closest ally is *victoriae* of South Australia, while *trilatera* is related to *gaimardi* of New Zealand. On the other hand, the *gilchristi-analogica* complex is close to the West African *rubicincta*. The relatives, possibly once-removed, of *alfredensis* and *trilatera* are the West African *madagascariensis* and *hyalina*, respectively. In the absence of fossil evidence, it is impossible to establish the ranges of the precursors of the *ponsonbyi-victoriae*, *alfredensis-albinella*, *trilatera-gaimardi* lineages, but it appears probable that these species once were widely distributed in the Indo-Pacific area and have been displaced and isolated in Africa, Australia, and New Zealand.

SYSTEMATIC SECTION

FAMILY TELLINIDAE

Gills small, posterior, not plicate, outer demibranch dorsally directed, reflected lamina obsolete or lacking; labial palps very large, more or less united posteriorly. Byssal apparatus obsolete. Foot compressed, short, and not grooved. Mantle margins papillose, with large ventral pedal gap. Siphons long, extensile, separate to their bases, and capable of retraction into extensive pallial sinus. Ligament external, opisthodetic, and generally subtended by nymphal callosities. Hinge with two cardinal teeth in each valve; lateral dentition present or absent. Cruciform muscles posterior.

Subfamily Tellininae

Shell narrowly or broadly lanceolate to ovate in shape, posterior side generally shorter, and often strongly flexed to right posteriorly. Valves usually of unequal convexity, left larger and more convex. Hinge with both cardinal and lateral teeth. Surface sculptured usually concentrically, generally heavier on rostral areas.

Genus *Tellina* Linnaeus

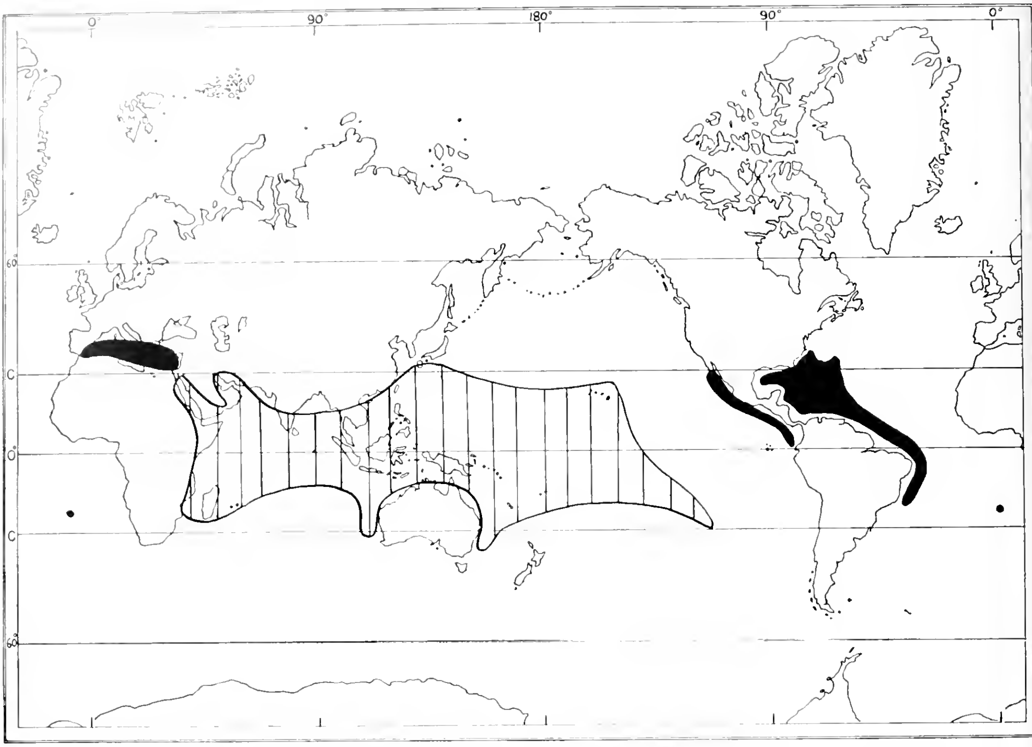
Tellina Linnaeus 1758, Syst. Nat., ed. 10: 674 (type-species, *Tellina radiata* Linnaeus 1758, subsequent designation Schmidt 1818: 51).

Description. Shell small to large, elliptical to ovate in shape, left valve generally more convex than right, variously flexed to the right posteriorly. Fragile to solid. Concentric sculpture predominant. Hinge with cardinal and lateral dentition. Cardinal teeth two in each valve: in the left valve, the anterior cardinal tooth is bifid and the posterior cardinal tooth is single and laminate; in the right valve, the anterior cardinal tooth is single and laminate and the posterior cardinal tooth is bifid. Lateral dentition variously developed, but lateral teeth of the right valve strong. Pallial sinus variously formed. Shell white to highly colored.

The correct type designation for the genus has been discussed by Boss (1966b). *Tellina sensu stricto* does not occur in South African waters. It is represented in the western Atlantic by such species as *T. radiata* Linnaeus and *T. brasiliana* Spengler, and in the Indo-Pacific by *T. chariessa* Salisbury (= *elegans* Gray).

Subgenus *Tellinella* Mörch

Tellinella Mörch 1853, Catalogus Conchyliorum . . . Comes di Yoldi, 2: 13 (type-species, *Tellina*



Map 3. The distribution of *Tellinella*. The species included are: in the Indo-Pacific, *virgata*, *staurella*, *crucigera*, *rastellum*, *pulcherrima*, *asperrima*, and *verrucosa*; in the western Atlantic, *listeri*; in the central Atlantic on St. Helena, *antonii*; in the eastern Pacific, *cumingii* and *zacae*; in the Mediterranean, *pulchella*. The group is largely of tropical distribution and, in the Indo-Pacific, replaces *Eurytellina* as a conspicuous element of the tellinid fauna.

virgata Linnaeus 1758, subsequent designation Stoliczka 1870: 116[1]).

Telinella Mörch. H. and A. Adams 1856, Genera Recent Mollusca, 2: 394, error for *Tellinella* Mörch.

Eutellina Fischer 1887, Manuel de Conchyliologie, p. 1147 (type-species, *Tellina virgata* Linnaens 1758, monotypy).

Tellinarius 'Froriep' Salisbury 1934, Proc. Mal. Soc. London, 21: 78 and 90 (type-species, *Tellina virgata* Linnaeus 1758, original designation), *non* Duméril 1806.

Description. Shell medium to large, ovate, elongate, or elliptical in outline, solid to subsolid, generally equivalve and nearly equilateral, more or less flexed to right posteriorly. Concentric sculpture developed, strong and often squamose posteriorly; radial sculpture rare. Lateral dentition developed in both valves. In right valve, both lateral teeth distal to the cardinal complex and strongly developed. In left valve, both lateral teeth distal to the cardinal complex and moderately developed. Ligament generally strong with subtending nymphal callosities. Pallial sinus linguiform and removed from anterior adductor muscle scar; confluence of pallial sinus and pallial line short and limited to the posterior half of the shell.

Remarks. Tellinella consists of a rather well-defined group of species that are characterized by having shells that are relatively strongly and lirately sculptured,

[1] The type-species is not *Tellina antonii* Philippi as indicated by Salisbury (1934), for Mörch did not cite any type-species in his use of the name *Tellinella*; the first known designation was made by Stoliczka.

with a complement of right lateral teeth more or less distally removed from the cardinal complex. The pallial sinus is rather extensive, extending near to the anterior adductor muscle scar and then falling in an irregular or subsigmoid arcuation to the pallial line, there to become confluent for about one half the length of the line posteriorly. Frequently an interlinear scar connects the pallial sinus and the anterior adductor muscle scar. The internal surface of the valves is usually rather highly polished and shining; nevertheless, the muscle scars are normally well impressed and easy to discern. Posteriorly, a complex of ridges and sulci are developed in conjunction with raised or stronger concentric sculpture and a more or less distinct flexure to the right.

The Indo-Pacific is the richest area in the world for the species of *Tellinella*. Largely tropical, usually conspicuous because of their brilliant coloration and considerable size, species of this group have been frequently collected, are well represented in collections, and are often taken in series. Of relatively shallow water habitat and often associated with the sandy areas around reefs, they are commonly encountered. Two more or less distinct species-complexes occur in the Indo-Pacific. On the one hand, there is the *T. virgata* complex, characterized by more or less regular concentric sculpture; on the other, the *T. rastellum* complex has the concentric sculpture raised, and broken into rasp-like structures. Both of the groups are widely distributed. In the western Atlantic, the well-known *T. listeri* occurs rather abundantly from North Carolina to Bahia, Brasil. The isolated population on St. Helena has been referred to *T. antonii* (Smith, 1890). The narrowly elongate, rather highly colored *T. cumingii* is found in the eastern Pacific. In the Mediterranean, the bright red, posteriorly pointed *T. pulchella* has been allocated to *Tellinella*. Map 3 shows the distribution of *Tellinella*.

Early fossil records of the group are from the Cretaceous of India (Stoliczka, 1870); later, it underwent a wide radiation in the Eocene of Europe and North America.

Tellina (Tellinella) virgata Linnaeus
Plate 2, figure 1; Plate 4, figure 1.

Tellina virgata Linnaeus 1758, Syst. Nat., ed. 10: 674; 1767, ed. 12: 1116 (type-locality, in O. Indico; type in collection of the Linnean Society, London[1]).

Tellina marginalis 'Lightfoot' Dillwyn 1817, Des. Cat., p. 74, *non* Lightfoot 1786.[2]

Tellina jubar Hanley 1844, Proc. Zool. Soc. London, pt. 12, no. 134: 60 (type-locality, unknown; syntypes, BMNH, unnumbered; labelled Swan River [Perth] and Montebello Ids., Western Australia); 1846 [*in*] Sowerby, Thes. Conch., vol. 1, *Tellina*, p. 229, pl. 63, fig. 214; Sowerby 1867 [*in*] Reeve, Conch. Icon., vol. 17, *Tellina*, figs. 48 and 48 b.

Description. Shell extending to 96 mm in length and to 56 mm in height, irregularly subtrigonal, slightly inequilateral, equivalved, subsolid to solid, somewhat inflated with left valve of greater convexity and with strong flexure to right posteriorly Umbo slightly behind middle, slightly elevated, rather inconspicuous and blunt. Anterior margin broadly rounded; ventral margin slightly convex, rising arcuately posteriorly; anterior dorsal margin straight to gently convex, elongate, and gently descending; posterior dorsal margin elongate, more steeply descending and straight; posterior margin irregularly biangulate, concave, and forming irregular oblique truncation posteriorly. Sculpture consisting of regularly spaced, rather well-developed, concentric lirations (3–4 per mm); extremely fine radial threads evident umbonally; concentric sculpture not smooth along posterior right dorsal slope and not highly

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[1] According to Hanley (1855: 33), the specimen figured by him in the Thesaurus Conchyliorum (1846), vol. 1, *Tellina*, pl. 63, fig. 204, is the type; this is construed to be a lectotype.

[2] Lightfoot's *marginalis* is based on a figure in Lister (1770: pl. 387) without reference to type-locality; it is a synonym of the common West Atlantic *T. laevigata* Linnaeus 1758. The Portland Catalogue and its valid names have been reviewed recently by Rehder (1967).

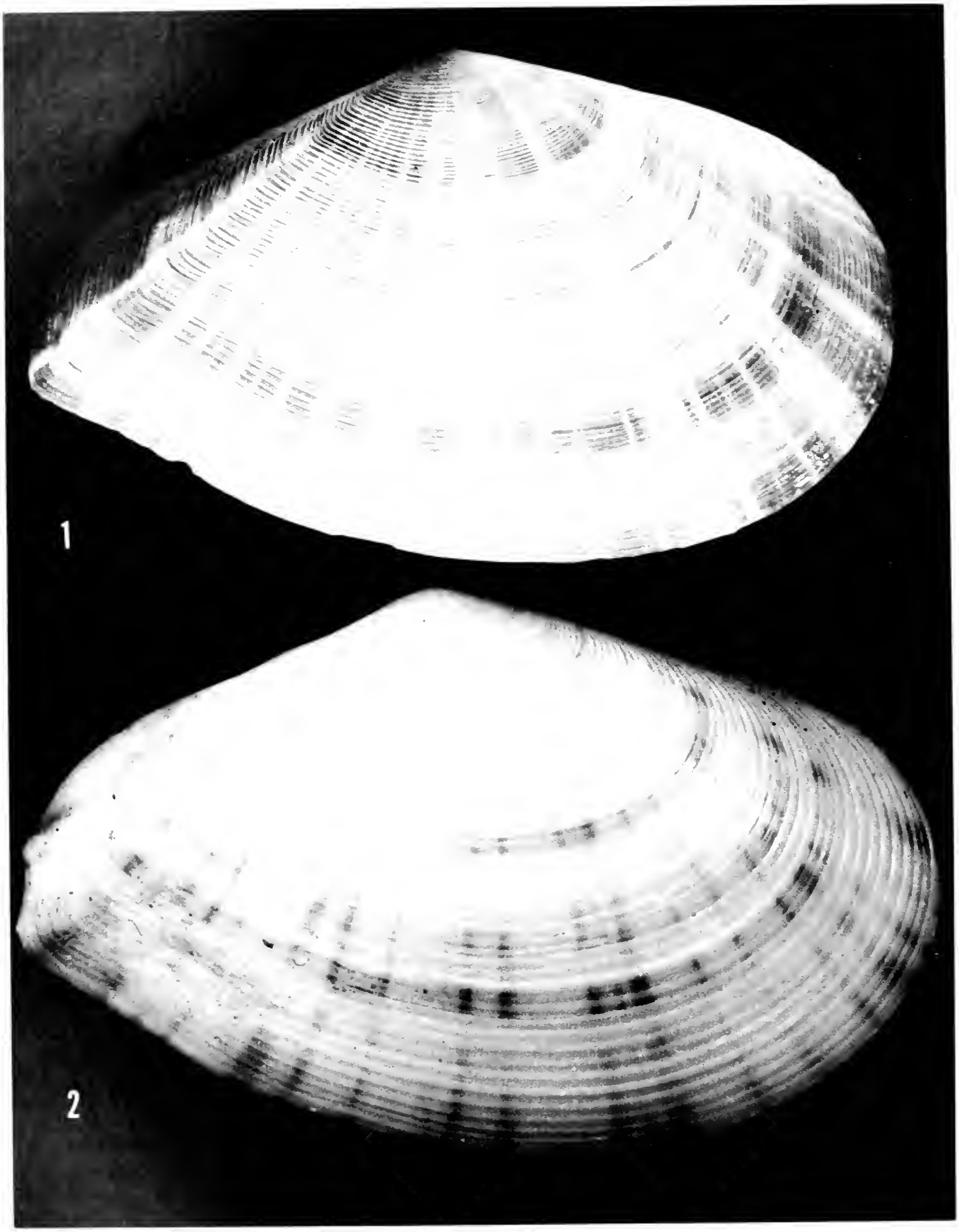

Plate 2. Fig. 1. *Tellina (Tellinella) virgata* Linnaeus: external view of the right valve, Durban, NM (length = 57.2 mm). Fig. 2. *Tellina (Tellinella) staurella* Lamarck: External view of the right valve, Apia, Upolu, Samoa, MCZ 235107 (length = 44 mm).

differentiated in right valve. Well-developed posterior ridge in right valve and concomitant sulcus in left valve.

Ligament generally yellowish brown, strong, protuberant, and elongate, set in weakly developed escutcheon; lunule consisting of poorly developed, depressed, semilanceolate area in right valve only; calcareous portion of ligament subtended by moderate to well-developed nymphal callosities. Hinge line well developed. In left valve, cardinal complex consisting of anterior, strong, subdeltoid, bifid tooth with subequal lobes, and of posterior, elongate, shelflike, thin, laminate tooth adpressed to base of calcareous portion of ligament; anterior lateral tooth distal to cardinal complex and consisting of thickened, somewhat pointed denticle of hinge margin; posterior lateral tooth obsolete, distal to cardinal complex; cardinal hinge plate extensive, particularly anteriorly. In right valve, cardinal complex consisting of posterior, slightly skewed, well-developed, bifid cardinal tooth with subequal lobes, and of anterior slightly thickened, laminate, cardinal tooth; anterior lateral tooth strong, shelflike, socketed above, and upcurled; posterior lateral tooth, strong, socketed above, pointed, slightly upcurled, and distal to cardinal complex; anterior lateral tooth closer to cardinal complex. No true rib present.

Muscle scars moderately well impressed; anterior adductor muscle scar irregularly semilunate; posterior adductor muscle scar subovate; ventral extension of posterior adductor muscle scar irregular. Pallial sinus subequal in opposite valves, arising at junction of ventral and lateral boundaries of posterior adductor muscle scar, rising subarcuately above, rounded anteriorly, and falling in convex arcuation to the pallial line; confluence posterior and irregular; pallial line with accessory pallial attachments paralleling it dorsally; pallial sinus connected to anterior adductor muscle scar by short, irregular interlinear scar. Cruciform muscle scars moderately developed, rounded, close to terminus of pallial line, left anteriormost subrectangular. Color basically white with suffusions of red, pink, orange, or yellow; externally with rays of white, or broken rays of red or pink and infrequently bands of red or pink; internally bands or rays showing through shells in immature individuals. In adults, interior highly polished; with central suffusions of yellow and white peripherally. Umbos generally red or pinkish.

Length mm	Height mm	Width mm	
95.7	55.1	22.7	Tuléar, Madagascar
75.2	45.4	19.3	Calatagan, Batangas, Luzon, Philippine Ids.
51.6	34.3	15.3	Lugger Cove, Western Australia
39.9	23.3	10.4	Apiang, Gilbert Ids.
27.1	16.0	06.5	Hayman Id., Queensland, Australia
21.5	13.5	05.0	Hayman Id., Queensland, Australia

Remarks. Probably the most cogent comments concerning *T. virgata* were presented by Rumph (1705), who not only established the meaningful and descriptive name of this species, but noted certain localities in the East Indies (e.g., Amboina and Ceram), the kinds of substrates it preferred, and the noticeable variations in shape and color it exhibited. His original illustration is here selected as type-figure. Although Linnaeus (1758) also cited a reference to Argenville, we are assured by Römer (1871) that in the manuscript for the 13th edition of the Systema, Linnaeus had deleted the reference to the illustrious Frenchman. In the published 13th edition, Gmelin (1791) managed to retain Argenville and expanded *virgata* to include the western Atlantic *T. listeri* Röding; he also cited Chemnitz (1782, pl. 8, figs. 66–72), who presented *virgata* in its range of variation, as well as *T. staurella*. Like Rumph, he also discussed the morphological variation. Shapes and color patterns were also recognized by Spengler (1798).

Since *T. virgata* is one of the most common tellens in the Indo-Pacific, it has been recorded in the literature numerous times.

Prashad (1932) had the stamina to ferret out its mention in checklists, dictionaries, encyclopedias, and other useful compilations, so he included, for the two specimens collected by the SIBOGA, over seventy bibliographic citations. More importantly, however, he came to the conclusion — safely based on the suggestion of Oostingh (1925) — that *jubar* Hanley and *marginalis* Dillwyn [= 'Lightfoot' Dillwyn, *non* Lightfoot] were based on only slight variations of *T. virgata*. A similar although somewhat earlier and independent conclusion had been reached by Römer (1871).

T. virgata is typically rounded anteriorly, with a pointed biangulate posterior margin. In color it is usually dull white, with variously disposed, red radiations that broaden from the umbonal region to the peripheral margins. The umbo is usually red or pink. Young stages of the shell are rounded in outline, with rather widely spaced, slightly raised concentric lirations and fine radial lines in the interstices, so that the sculptural pattern is cancellate. From the closely related *T. staurella*, *virgata* may be distinguished by the row of accessory pallial attachment muscle scars that parallel the pallial line on the internal surface of the valve. The pallial sinus is often not distinctly confluent. The ventral extension of the posterior adductor muscle scar is irregular and usually not broadly coextensive. The pallial sinus connects with the posterior adductor muscle scar at the junction of the ventral and lateral portions of the scar and usually not on the medial lateral surface. There are further, though somewhat more ephemeral, distinctions: the shell of *virgata* is thinner and less heavy, the concentric sculpture on the anterior slope is stronger, sharper, and more closely spaced, the cardinal and hinge plates are thicker and dorso-ventrally larger, and the maximum total size of *virgata* is larger than that of *T. staurella*.

Range. Tellina virgata, a relatively common shallow water species that prefers sandy substrates, occurs from Natal, South Africa, throughout the Indian Ocean, Indonesia, the Philippine Islands, Melanesia, to Tahiti in the Society Islands. It has been taken south to Shark's Bay in western Australia and as far north as Okinawa in the Ryu Kyu Islands.

Specimens examined. REPUBLIC OF SOUTH AFRICA: Natal (USNM). MOZAMBIQUE: Mozambique City; Porto Amélia (both USNM). TANZANIA: Mboa Maji, 9 mi. S of Dar-es-Salaam (USNM); Zanzibar (BMNH); 1 mi. N of Paje, 1 mi. SW of Nguruwe Id., Pwani Mehangani, and Mazizini, Zanzibar (all ANSP). RED SEA: (MCZ). MADAGASCAR: Tuléar (MCZ); between Ambatoloaka and Madirokely, SW of Nossi Bé and Befotake, NW of Nossi Bé (both ANSP). SEYCHELLES IDS.: Anse Parnel, Mahé (BMNH). MAURITIUS: S side of Tombeau Bay, 1 mi. NE of Le Morne, and Flic en Flacq (all ANSP). MALDIVE IDS.: Miladummadulu Atoll, S half of Kendikolu Ids. (5°57'N; 73°24'E) (ANSP). CEYLON: (MCZ). ANDAMAN IDS.: Port Blair (DM; MCZ). MALAYSIA: Singapore (ANSP); Palau Hautu, SW Keppel Harbor (USNM). THAILAND: Koh Samui (USNM). INDONESIA: Java (MCZ); Denpasar, Bali (USNM); Koeta Beach, Bali (MCZ); Semporna Reef, Sibuan Id., and Mandibarrah Id., N. Borneo (all ANSP; USNM); Misool Id.; Amboina; Tengah Id., off Buru; Banda Nera; Jamna Id., New Guinea (all MCZ); E side of Rouw Id., Aoeri Ids., Geelvink Bay, New Guinea (ANSP). CHINA: Kanna (MCZ); Plover Cove, near Hong Kong (ANSP). JAPAN: Abu, Ishikawa Beach, Ora Wan, Itoman Shioya, all Okinawa, Ryu Kyu Ids. (all USNM). PHILIPPINE IDS.: E coast of Polillo; Manila, Luzon; Subic Bay, Zambales, Luzon; Calatagan, Batangas, Luzon (all USNM); E side of Sisiman Bay, Bataan; SW side of Talin Bay, Luzon; Badang, near Gubat, Luzon (all ANSP); Gigmoto, Catanduanes (ANSP); Tilic Bay, Lubang; Calapan, Mindoro; Catbalogan, Samar; (all MCZ); Cebu City, Cebu; E side of Jago-

lias Id., NW end of Bohol; Zamboanga, Mindanao (all ANSP); Malcochin Harbor, Linapacan Id., N of Palawan; Palawan (both MCZ); Makesi Id., off Palawan; Port Ciego, Balabac; Tawi Tawi Group (all USNM); Bongao Channel, SW end of Sanga Sanga Id. (ANSP). AUSTRALIA: Lugger Cove, Shark's Bay, and Augustus Id., Western Australia (both MCZ); Port Essington, Coburg Peninsula, Northern Territory; Bickerton Id., and NE end of Groote Eylandt, Gulf of Carpentaria (all USNM); Cooktown, Queensland (MCZ); Palm Id., Challenger Bay (ANSP); Dunk Id. (ANSP; BMNH); Brampton Reef and Port Denison, off Bowen Id. (both USNM); Stone Id. (ANSP); Gloucester Id., Whitsunday Group (USNM); Hayman Id., Cumberland Group, Whitsunday Passage (MCZ); near Gladstone (USNM). PALAU IDS.: Schonian Harbor, Peleliu Id. (ANSP). MARIANA IDS.: Tanapag Harbor, Saipan (ANSP; USNM); Apaca Point, Agat Bay, Guam (ANSP). MARSHALL IDS.: Pokaakku Atoll (USNM). GILBERT IDS.: Apiang, Kingsmill Group (MCZ; USNM). LOYALTY IDS.: Lifu (USNM). NEW CALEDONIA: Paagoumene; Plage de Poe; Pt. Akaia, Bourail; Tonghouen; Anse Vata Bay, Noumea (all ANSP). FIJI IDS.: Suva, Titi Levu (MCZ; USNM); Bega Id. (MCZ); Komo, Lau Group (USNM). SAMOA IDS.: Pago Pago Harbor, Tutuila (MCZ; USNM); Toloa Point, Upolu Id. (ANSP). TONGA IDS.: Vavau (BMNH); Haapai (USNM). COOK IDS.: W side of Akitua, NE Aitutaki (ANSP). SOCIETY IDS.: Tereia Point, Bora Bora (ANSP); Tahiti (USNM).

Tellina (*Tellinella*) *staurella* Lamarck
Plate 2, figure 2; Plate 3, figures 1, 2; Plate 4, figure 2.

Tellina cruciata Spengler 1798, Skrivter af naturhistorie Selskabet, København, 4 (2): 83 (type-locality, Fra Niquebar; types, ? Zoological Museum, Copenhagen), *nomen dubium*.

Tellina staurella Lamarck 1818, Anim. sans Vert., 5: 522 (type-locality, . . . Nouvelle Holland; syntypes, MNHNP, *teste* Bertin 1878: 236); Delessert 1841, Rec. Coq., pl. 6. fig. 2.

Tellina scalaris Lamarck 1818, Anim. sans Vert., 5: 527 (type-locality, unknown; holotype, MNHNP, *teste* Bertin 1878: 236).

Tellina incerta Deshayes 1854, Proc. Zool. Soc. London [1855] pt. 22, no. 282: 367 (type-locality, Philippines [Islands]; syntypes, BMNH, unnumbered); Sowerby 1867 [*in*] Reeve, Conch. Icon., vol. 17, *Tellina*, pl. 38, fig. 217.

Tellina petalina Deshayes 1854, Proc. Zool. Soc. London [1855] pt. 22, no. 282, p. 367 (type-locality, unknown; holotype, BMNH, unnumbered).

Tellina rufa Deshayes 1854, Proc. Zool. Soc. London [1855] pt. 22, no. 282: 367 (type-locality, unknown; holotype, BMNH, unnumbered); Sowerby 1869 [*in*] Reeve, Conch. Icon., vol. 17, *Tellina*, pl. 57, fig. 337.

Tellina petallina Deshayes. Sowerby 1868 [*in*] Reeve, Conch. Icon., vol. 17, *Tellina*, pl. 49, fig. 292, error for *petalina* Deshayes 1855.

Tellina (*Tellinella*) *staurella apicifusca* (Jousseaume MS) Lamy 1918, Bull. Mus. Natl. Hist. Nat. Paris, 24: 27 (type-locality, Massaouah, Djibouti; types, ? MNHNP; refers to Chemnitz 1782, 6: 86, pl. 8, fig. 70).

Tellina acropisthus Barnard 1964, Ann. Natal Mus., 16: 26, fig. 5b (type-locality, off Cape Natal (Durban); syntypes, SAM 9547).

Description. Shell extending to 65 mm in length and to 37 mm in height, subelliptical, pointed behind, rather equilateral and equivalved, rather solid and slightly inflated, with left valve slightly more convex than right, and with moderate flexure to right posteriorly. Umbo central or slightly behind middle, relatively inconspicuous, small, pointed, and slightly elevated. Anterior margin rather narrowly and smoothly rounded; ventral margin gently convex and rising in slight arcuation posteriorly; anterior dorsal margin straight to slightly convex, rather long, and gently descending; posterior dorsal margin slightly concave, more steeply descending, and shorter; posterior margin irregularly biangulate, forming irregular oblique truncation. Sculpture consisting of finely incised, slightly raised lirations (2–3 per mm); radial vermiculations sometimes evident; concentric sculpture often subscissulate[1]

[1] The terms scissulate, scissulation, etc., have been defined by Boss and Kenk (1964) and Boss (1966a).

Plate 3. Figs. 1 and 2. *Tellina (Tellinella) acropisthus* Barnard [= *T. staurella* Lamarck], the holotype, off Cape Natal, Durban, SAM A9547 (length = 14.6 mm): Fig. 1, external view of the right valve; Fig. 2, internal view of the right valve. Figs. 3 and 4. *Tellina (Tellinella) rastellum* Hanley, Durban, NM (length = 42.5 mm): Fig. 3, external view of the right valve; Fig. 4, internal view of the right valve.

along posterior dorsal slope of left valve and often lost or obsolete in that area, forming indistinct or strongly developed, radial, smooth band from umbo to ventral margin at junction of posterior and ventral margins. Posterior ridge biangulate and rather well developed in right valve; concomitant sulcus in left valve.

Ligament yellow to dark brown, rather strong, slightly protuberant, broad, elongate, and set in a weakly developed, elongate, sublanceolate escutcheon; lunule obsolete, developed somewhat in right valve, elongate and lanceolate; calcareous portion of ligament set on short, slightly raised nymphal callosities. Hinge line well developed. In left valve, cardinal complex consisting of anterior, subdeltoid, bifid tooth with irregular lobes, and of posterior, thin, short, laminate cardinal tooth adpressed to base of calcareous element of ligament; anterior lateral tooth distal to cardinal complex, poorly developed, consisting of blunt thickening of hinge line; posterior lateral tooth obsolete, distal, and consisting of weak thickening of hinge line; cardinal plate rather narrow, with irregular proximal thickening infrequently occurring in hinge line anterior to cardinal complex. In right valve, cardinal complex consisting of posterior subdeltoid, posteriorly skewed, bifid cardinal tooth with subequal lobes, and of anterior thickened to subdeltoid laminate cardinal tooth; anterior lateral tooth strong, shelflike, upcurled, and socketed above; posterior lateral tooth slightly less well developed, socketed above, upcurled and shelflike; anterior lateral tooth closer to cardinal complex; posterior lateral tooth distal. No true rib developed.

Muscle scars moderately well developed, impressed and conspicuous; anterior muscle scar broadly and irregularly sublunate; posterior scar subquadrate to subovate; posterior extension of posterior adductor muscle scar broadly coextensive with adductor scar. Pallial sinus subequal in opposite valves, arising from lateral surface of posterior adductor muscle scar, coursing straight anteriorly in gentle arcuation, rounded anteriorly, and falling in a semi-

sigmoid arcuation to the pallial line; confluence about one half length of pallial line; no accessory pallial muscle scars paralleling pallial line. Cruciform muscle scars moderately developed, rounded, with anteriormost scar in left valve subquadrate. Color basically white, externally with bands of purple and white rays or red suffusions; infrequently, shell entirely suffused with purple or yellow; internal suffusions of yellow common. Umbo white or often red and infrequently streaked with brilliant red.

Length mm	Height mm	Width mm	
64.2	37.0	17.4	Zanzibar, Tanzania
38.6	25.2	12.6	Bay of Batavia, Java, Indonesia
36.4	23.4	11.5	Ibajay, Panay, Philippine Ids.
26.7	15.8	07.1	Calapan, Mindoro, Philippine Ids.
21.6	12.3	05.7	Calapan, Mindoro, Philippine Ids.
10.7	06.6	03.1	Guiuan, Samar, Philippine Ids.

Remarks. Due to its remarkable range of variation, *T. staurella* may be easily confused with the closely related tellinelloid species of the Indo-Pacific, *T. virgata* and *T. crucigera.* The most variable characteristic appears to be shell color. Most specimens are in the yellow-white spectrum, with suffusions of yellow concentrated centrally and umbonally; the internal surfaces of the valves are normally polished and shining, and the periphery is whitish. However, a number of names have been established on the deep purple variants, those with brilliant red streaks on the umbo, and others with variously developed red or pink radiations. Not infrequently, pure white individuals occur.

The concentric sculpture of *T. staurella* is well developed. It is usually strengthened posteriorly, whereas on the anterior slope of the disc it tends to be moderately sulcate. Along an axis from the umbo to the junction of the posterior and ventral margins on the posterior slope of the right valve, the rather widely spaced concentric lirations may suddenly fade out, forming a radial band of various widths, which is smooth and devoid of any noticeable sculpture. The concentric sculpture on the disc may end abruptly or simply become much weaker; it also may tend to be slightly acentric or subscissulate. However, not all individuals in a population have the smooth posterior radial band. Specimens with the band and those without were often considered as separate species, and the absence of any smooth area on the right posterior slope in the shell of *T. virgata* was used to distinguish that species. Since both extremes and all intermediates occur in *T. staurella,* such a trait is unsatisfactory as a diagnostic characteristic.

T. staurella differs from *T. virgata* in a number of general aspects. Bertin (1878) detailed some of these differences, but they are rather difficult if not impossible to quantify and are frequently not stable. In general appearance, *T. staurella* is more elongate, more narrowly rounded anteriorly, and less pointed or biangulate posteriorly. The species has a weaker, less thickened hinge line, is more heavily shelled, and is less densely sculptured — in adults — than is *T. virgata.* In addition to these less than ideal differentiating characteristics, *T. staurella* has a simple pallial line without accessory pallial attachments, and the ventral extension of the posterior adductor muscle scar is strongly impressed and broadly connected with the muscle scar. The pallial sinus tends to connect with the posterior muscle scar on the lateral surface of that scar. Further, as explained in the *Remarks* under *T. virgata,* the young of *T. staurella* are not distinctly cancellate and have closely set concentric lirations.

Range. Tellina staurella is a common species found in relatively shallow water, usually in rather coarse substrates from Durban, South Africa, throughout the Indian Ocean, Indonesia, the Philippine Islands, Melanesia, to the Tonga Islands in Polynesia.

Specimens examined. REPUBLIC OF

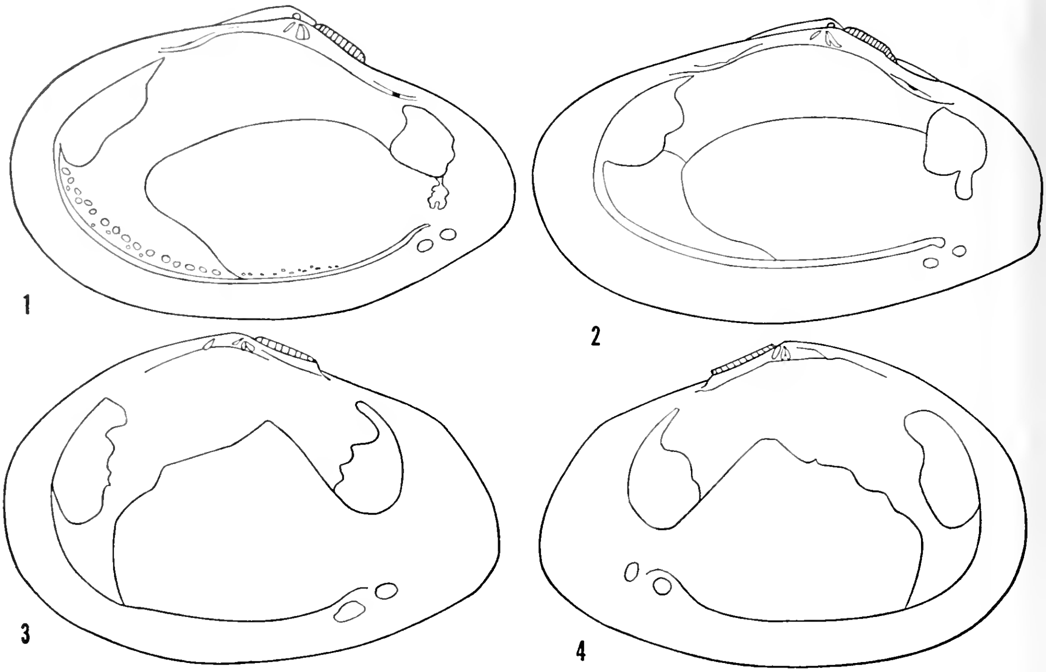

Plate 4. Diagrammatic illustrations of the internal surface of the valves, showing the dental configuration and muscle scars. Fig. 1. *Tellina* (*Tellinella*) *virgata* Linnaeus: right valve, Hayman Island, Whitsunday Passage, Queensland, Australia, MCZ 257176 (length = 21 mm). Note the distinct accessory pallial attachment muscle scars. Fig. 2. *Tellina* (*Tellinella*) *staurella* Lamarck: right valve, Calapan, Mindoro, Philippine Islands, MCZ 257177 (length = 21.6 mm). Figs. 3 and 4. *Tellina* (*Tellinides*) *apalina* Gmelin, Delagoa Bay, Mozambique, SAM A6181 (length = 29 mm): Fig. 3, right valve; Fig. 4, left valve.

SOUTH AFRICA: Durban (DM; NM; SAM; USNM). MOZAMBIQUE: Santa Carolina Id., Bazaruto Bay (MCZ); Lumbo (BMNH; MCZ); Porto Amélia (USNM). TANZANIA: Mboa Maji, 9 mi. S of Dar-es-Salaam (USNM); Bweleo and Bweju, Zanzibar (both USNM); Mazizini, Zanzibar (ANSP). KENYA: Diana Beach, 20 mi. S of Mombasa (USNM). SOMALIA: Isla di Serpenti, Chisimaio (ANSP). RED SEA: (MCZ). SAUDI ARABIA: Jidda Harbor (USNM). ADEN PROTECTORATE: Aden (BMNH). MADAGASCAR: Nossi Bé (MCZ); W of Pointe Mahatsinjo, S of Nossi Bé; Nossi Kisimani, 12 mi. SSW of Nossi Bé; N end of Nosy Kalakajoro, Iles Radama, 52 mi. SSW of Nossi Bé; 3 mi. NNE of Nossi Fali (all ANSP). SEYCHELLES IDS.: Mahe in 4–11 fms. (BMNH). MAURITIUS: Near Port Louis (BMNH; MCZ). CEYLON: (ANSP; MCZ; USNM). ANDAMAN IDS.: Port Blair (BMNH). NICOBAR IDS.: (ANSP). MALAYSIA: Singapore (BMNH; MCZ; USNM). THAILAND: 3 mi. NE of lighthouse, Laam Phan Wa, and airport beach, Phuket Id. (all ANSP); Goh Sindarar Nui [= Chance Id.] (USNM). INDONESIA: Pulau Melila and Pulau Bai, Batu Group, off Sumatra (both USNM); Bay of Batavia, Java (MCZ); Sandakan, Sabang, Jesselton, Semporna Reef, and Mandibarrah Id., all N. Borneo (all ANSP; USNM); Bali; Wawoni Id., off Celebes; Misool; Karakelong Id., Talauer Ids.; Buru; Tengah Id., off Buru; Amboina; Laratoeka Straits, Flores Ids. (all MCZ); near Gamododo, Milne Bay, New Guinea (USNM);

2 mi. W Korido Village, Soepiori Id., Schouten Ids.; Ambai, Japen Id.; S side of Rouw Id., Aoeri Ids., Geelvink Bay, New Guinea (all ANSP). JAPAN: Sagami Bay, Honshu (ANSP); southern Kyushu (ANSP); Gima, Kumejima Id., Okinawa (ANSP); Abu, Kanna, Nago, and Shuri, all Okinawa, Ryu Kyu Ids. (all USNM). PHILIPPINE IDS.: Sabtan Id., Batanes Group (USNM); Camiguin Id. (USNM); Masinloc Bay, Zambales, Luzon (USNM); Baga Bay and Sisiman Bay, Mariveles, Bataan, Luzon (ANSP; USNM; MCZ); in 11 fms., off Corregidor; 4 mi. SW of San Nicholas Shoals Light, Manila Bay, Luzon; SW side of Talin Bay and Calatagan, Batangas, Luzon; Badang, near Gubat, Sorsogon, Luzon (all ANSP); Cabila Point, Cueva, and the Tilic Bay (all Lubang) (USNM; MCZ); Gigmoto, Catanduanes (ANSP); Calapan, Mindoro (MCZ; USNM); Santa Crux Harbor, Marinduque; San Pascual, Burias; Busuanga (all USNM); Gyo, Palawan (ANSP); Araceli, Dumaran Id., off Palawan (MCZ); Cagayancillo, Cagayanos Ids. (USNM); Calbayog, Samar Id.; Guiuan, Samar Id.; Ibajay, Panay (all MCZ); Cebu; Mantacas Id., off Bohol (both USNM); Mambajao, Camiguin Id., N of Mindanao (ANSP); Davao, Mindanao (MCZ); Tawi Tawi Group (USNM); Bongao Channel, Sanga Sanga Id. (ANSP). AUSTRALIA: Augustus Id., NW Australia (MCZ); Torres Straits; Trinity Bay (both BMNH); Michaelmas Cay, Green Id., near Cairns (MCZ); Brampton Reef, off Bowen Id. (USNM); Hayman Id. and Langford Reef, Whitsunday Group (MCZ). PALAU IDS.: W end of Gorokoru; Malakal Harbor, Koror; SE corner of Eil Malk (all ANSP). MARIANA IDS.: Piti Bay and Agana Bay, Guam (MCZ; USNM). CAROLINE IDS.: Tomil Harbor, Yap (USNM). MARSHALL IDS.: off SW end of Bikini (USNM). GILBERT IDS.: Apiang, Kingsmill Group (MCZ). BISMARCK ARCHIPELAGO: Kaniet, Admiralty Ids. (ANSP). SOLOMON IDS.: Buin, Bougainville (ANSP); Roviana Lagoon, New Georgia (MCZ); Ata'a, Malaita (ANSP). NEW CALEDONIA: Koë Reef, 2 mi. SSE of Touho; Ile Ain, 3 mi. ENE of Touho; SE side of Touho Bay; Bourail; off Gatope Id.; Port Ngea, Magenta, Baie des Canards, Anse Vata Bay; Ricaudy Reef, near Noumea (all ANSP). FIJI IDS.: Yasawa Group (USNM); Bega Ids. (MCZ); off Suva and off Nandronga, Viti Levu (both USNM); off Tunuloa and off Natuvu, Vanua Levu (both MCZ); Komo, Lau Group (USNM). SAMOA IDS.: W side of Apia Harbor, Vailele Bay, and Samatau, all Upolu; Pago Pago Harbor, Tutuila (all ANSP). TONGA IDS.: Tongatapu, Tukutonga Reef, E of Nukualofa (USNM).

Tellina (*Tellinella*) *rastellum* Hanley
Plate 3, figures 3, 4; Plate 5, figures 1, 2.

Tellina rastellum Hanley 1844, Proc. Zool. Soc. London, pt. 12, no. 134: 59 (type-locality, Zanzibar; syntypes, BMNH, unnumbered); [1842–1856], Recent Bivalve Shells, Appx., p. 347 [1856], pl. 14, fig. 14 [1844]; 1847 [*in*] Sowerby, Thes. Conch., vol. 1, *Tellina*, p. 225, pl. 64, fig. 231, pl. 65, fig. 242.

Tellina philippii (Anton MS) Philippi 1844, Abbild. Beschreib. Conch., vol. 1, *Tellina*, pl. 2, p. 126 [4], fig. 8 (type-locality not given; types not known).

Tellina dissimilis Deshayes 1854, Proc. Zool. Soc. London [1855], pt. 22, no. 283: 370 (type-locality not given; syntypes, BMNH, unnumbered); Sowerby 1869 [*in*] Reeve, Conch. Icon., vol. 17, *Tellina*, pl. 56, figs. 338 a-b, *non* von Martens 1865.

Description. Shell extending to 103 mm in length and to 51 mm in height, elongate-sublanceolate, nearly equilateral, subequivalve, solid, rather compressed, with left valve of slightly greater convexity, and with posterior flexure to right. Umbos central or slightly behind middle, not elevated, somewhat pointed; umbonal cavity shallow and sometimes filled. Anterior margin smoothly and narrowly rounded; ventral margin gently convex, rising in concave arcuation posteriorly; anterior dorsal margin long, gently descending, and weakly convex; posterior dorsal margin equally as

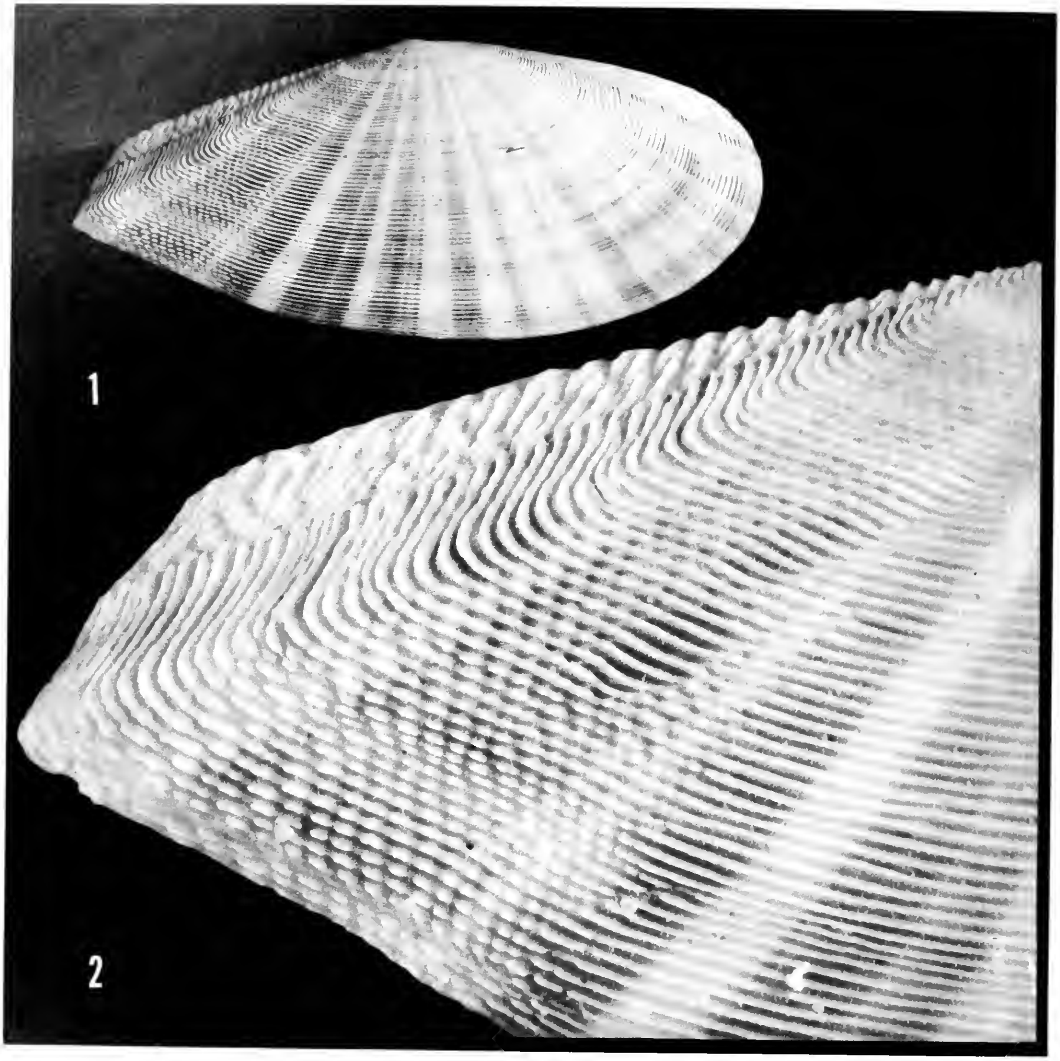

Plate 5. *Tellina* (*Tellinella*) *rastellum* Hanley, Mozambique, USNM 628938 (length = 88.3 mm). Fig. 1. External view of the right valve. Fig. 2. Enlargement of Figure 1, to show the rasplike sculpture on the posterior slope.

long, somewhat more sharply descending and rather straight; posterior margin oblique, subdivided into dorsal and ventral portions, each irregularly concave. Concentric sculpture consisting of narrow, raised, and regularly spaced lirations (about 14–17 per cm in adult specimens), becoming stronger and differentiated along posterior slope. Area of strengthened sculpture greater in right valve. Differentiation consisting of sharply raised lirations, irregularly spaced concentrically, and forming rasplike structures along posterior slope. Lirations also somewhat stronger on anterior slope, but not differentiated into thin, rasplike pattern. Extremely fine, regularly spaced, radial sculpture most evident on umbonal region of disc, but also discerned in deep sulci or interspaces separating concentric lirations. At least two strong posterior

radial ridges in right valve; similar ridges in left valve, but not as strongly differentiated. Irregular, rather deep sulcus separating ridges in right valve. Concentric sculpture sharp, sublamellose over ridges; generally rasps absent.

Ligament strong, dark brown to black, protuberant, and somewhat set in indistinct lanceolate escutcheon; no true lunule, but elongate, depressed, anterior area stronger in right valve. Calcareous portion of ligament elongate and narrowed, subtended by slightly raised nymphal callosities. Hinge line strongly developed. In left valve, cardinal complex consisting of strong, subdeltoid, bifid anterior tooth with subequal lobes, and of posterior narrowed, laminate tooth closely adpressed to calcareous portion of ligament; both cardinal teeth often lost in large adult specimens; lateral teeth moderately developed, shelflike thickenings of hinge line, bluntly pointed; anterior lateral stronger and distal to cardinal complex, but closer than posterior lateral tooth. In right valve, cardinal complex consisting of posterior strong, subdeltoid, bifid tooth with lobes often skewed posteriorly, and of anterior strong, narrowed tooth; lateral dentition strong, socketed above, pointed, and upcurled; anterior lateral tooth closer to cardinal complex than posterior lateral tooth, but both somewhat distally removed.

Muscle scars rather well impressed. Anterior adductor muscle irregularly semilunate, round ventrally; posterior adductor muscle scar subquadrate with small ventral extension. Pallial sinus more or less equal in opposite valves, rising only slightly posteriorly, then gently and regularly descending, bluntly pointed anteriorly, then descending in convex arcuation and forming confluence with pallial line for posterior half of shell length; anteriormost portion of pallial sinus connected to anterior muscle scar with interlinear scar; pallial sinus itself well removed from anterior scar; confluence of pallial sinus and pallial line shorter in right valve. Cruciform muscle scars moderately impressed, generally rounded, closely juxtaposed in right valve, somewhat more widely separated in left valve, and with anterior scar slightly flattened or subrectangular. External color white to yellow, with reddish rays of various widths and numbers. Internally polished, with external radial patterns showing through shell, and often central and umbonal suffusions of yellow.

Length mm	Height mm	Width mm	
102.8	50.5	22.1	The Bluff, Durban
83.7	36.7	15.8	Porto Amélia, Mozambique
74.3	34.6	14.7	Porto Amélia, Mozambique
61.0	26.4	11.8	Bawi Id., Zanzibar
48.5	19.8	07.9	Durban
43.1	17.5	07.1	Durban

Remarks. Among the Tellinacea, and certainly within the Tellininae, *T. rastellum* is one of the species with the largest dimensions. No other member of *Tellinella* exceeds it in size, and only *Tellina* (*Laciolina*) *magna* from the western Atlantic is larger in overall length.

Unfortunately, a complete ontogenetic series of this species is not available. However, as in many other tellinoid species, *T. rastellum* exhibits differences of proportions between the smaller or more immature specimens and the larger adults. As the measurements indicate, individuals of shorter length tend to be proportionately of less height. That is, immature specimens are narrower and more lanceolate in outline. Deshayes (1855) established his *T. dissimilis* on the young of *T. rastellum.*

A number of Indo-Pacific species of *Tellinella* have peculiar rasplike sculpture; they are all relatives of *T. rastellum.* These include *T. pulcherrima* Sowerby 1825, *T. asperrima* Hanley 1844, and *T. verrucosa* Hanley 1844. Prashad (1932) has given a complete historical résumé of these species. Smith (1885) noted the resemblance between species with the rasplike sculpture, which differ chiefly in the extent of the distribution of this sculpture over the surface of the valves. In *rastellum,* the rasps are developed posteriorly, whereas in

pulcherrima, both the anterior and posterior slopes have them; in *asperrima* and *verrucosa*, the entire valve surface, including the central area of the disc, has this sculpture. The relative proportions of the shell differ in these species. *Tellina rastellum* is distinct in having the umbo central or slightly behind the middle. Further, its rasps are not present on the extreme posterior dorsal slope, the area set off by the radial ridges.

Range. From all available evidence, there may be two disjunct populations of *T. rastellum*. One, the more extensive, occurs from the Persian Gulf through the Arabian Sea and Indian Ocean south along the coast of East Africa to the vicinity of Durban, Natal, South Africa. Offshore islands, including the Seychelles and Madagascar, are also inhabited by this western population. The other population ranges through Indonesia and the northern Philippines to the Palau Islands of the western Caroline Islands.

Numerous authors have documented the occurrence of *T. rastellum* through the range delineated above. The following is a selected bibliography of records of this species. Natal (Sowerby, 1897); Ponta Torres (Paes da Franca, 1960a); Inhaca (Boshoff, 1965); Kerimba (von Martens, 1880); Madagascar (Bertin, 1878; Dautzenberg, 1929); Seychelles (von Martens, 1880); Dar-es-Salaam (Spry, 1964); Zanzibar (Römer, 1871); Djibouti, Périm, Aden (Lamy, 1918); Red Sea (Issel, 1869); Attaka (Vaillant, 1865); Gulf of Oman, Muskat (Melvill and Standen, 1907); Minikoy, Maldive Islands (Smith, 1906); Philippines (Hidalgo, 1903). The species has also been found fossilized in the Quaternary deposits along the Red Sea (Bertin, 1878; Nardini, 1937).

Specimens examined. REPUBLIC OF SOUTH AFRICA: The Bluff, Durban (NM); Durban Beach (USNM); Durban Bay (DM; NM); Natal (BMNH; MCZ). MOZAMBIQUE: Inhaca Island (ANSP); Mozambique City (ANSP); near Porto Amélia (USNM). TANZANIA: Chumbe Island; 1 mi. N of Paje in 0–10 ft. (0–3 m); Mazizini; Mkunguni; Mnemba Island in 0–6 ft. 0–1.8 m); Ras Nungwe, Zanzibar (all ANSP); Bawi Island (USNM). ADEN PROTECTORATE: Aden (BMNH). MADAGASCAR: 3 mi. SE of Nosy Iranja in 11 fms. (20 m), sand; Andilana, Nosy Bé in 0–5 ft. (0–1.5 m), mud, sand and rock (both ANSP). INDONESIA: Padang, Sumatra (BMNH), PHILIPPINE ISLANDS: S side of Corregidor Island, Luzon in 11 fms. (20 m) (ANSP). CAROLINE ISLANDS: off Arakabesan Island, Palau Islands (ANSP).

Subgenus *Arcopagia* Brown

Arcopagia (Leach MS) Brown 1827, Illus. Conch. Great Britain and Ireland, pl. 16, figs. 8, 9, 10 (type-species, *Tellina crassa* Pennant 1776, subsequent designation Herrmannsen, 1846, p. 76).

Cydippe (Leach MS) Gray 1852, Syn. Moll. Great Britain, p. 314 (type-species, *Cydippe listeriana* Leach 1852 [= *Tellina crassa* Pennant 1776], monotypy), *non* Eschscholtz 1829 (Coel.).

Arcopagia '(Leach MS) Brown' von Martens 1860, Proc. Zool. Soc. London, pt. 28 [1], p. 18, error for *Arcopagia* (Leach MS) Brown 1827.

Arcopogia '(Leach MS) Brown' Guéranger 1867, Album Paléont. Sarthe, p. 12 and explan. pl. xv, fig. 11, error for *Arcopagia* (Leach MS) Brown [original not seen, *teste* Neave 1939, p. 283].

Acropagia '(Leach MS) Brown' Carus 1868–75 [*in*] Carus, J. V. and C. E. A. Gerstaecker, Handbuch Zool., 1: 734, error for *Arcopagia* (Leach MS) Brown 1827.

Arcopagella Meek 1871, Prelim. Rept. U. S. Geol. Surv. Wyoming and Territories, p. 308 (type-species, *Arcopagella mactroides* Meek 1871, monotypy).

Pseudarcopagia Bertin 1878, Nouv. Arch. Mus. Paris, Sér. 2, 1: 229, 264 (type-species, *Tellina decussata* Lamarck 1818, *non* Wood 1815 [= *victoriae* Gatliff and Gabriel 1914], subsequent designation Dall 1900: 1011).

Cyclotellina Cossmann 1886, Ann. Soc. R. Malac. Belg., 21: 79 (type-species, *Tellina lunulata* (Lamarck MS) Deshayes 1824, original designation).

Arcopagiopsis Cossmann 1886, Ann. Soc. R. Malac. Belg., 21: 81 (type-species, *Tellina pustula* Deshayes 1825, subsequent designation, Dall 1900: 1005).

Pseudoarcopagia 'Bertin' Tate and May 1901, Proc. Linn. Soc. New South Wales, 26 (3): 426, error for *Pseudarcopagia* Bertin 1878.

Arcopaginula (Jousseaume MS) Lamy 1918, Bull. Mus. Natl. Hist. Nat. Paris, 24: 167 (type-species, *Tellina inflata* Chemnitz 1782 [= *T. inflata* Gmelin 1791], *non* Sowerby 1867, original designation).

Scutarcopagia Pilsbry 1918, Proc. Acad. Nat. Sci. Philadelphia, 69: 332 (type-species, *Tellina scobinata* Linnaeus 1758, original designation).

Pinguitellina Iredale 1927, Rec. Australian Mus., 16: 76 (type-species, *Tellina robusta* Hanley 1844, original designation).

Zearcopagia Finlay 1927, Trans. Proc. New Zealand Inst., 57: 466 (type-species, *Tellina disculus* Deshayes 1855, original designation).

Arcopella (Monterosato MS) Thiele 1935, Handbuch der systematischen Weichtierkunde, vol. 2, pt. 3: 914 (type-species, *Tellina balaustina* Linnaeus 1758, monotypy).

Description. Shell small to large, usually ovate, solid, equivalve, and more or less equilateral. Lateral dentition well developed. In right valve, both lateral teeth distinct and strong; posterior lateral tooth distal to cardinal complex and anterior lateral tooth subproximal or distal to cardinal complex. Pallial sinus of various configurations; sometimes linear scar connecting anterior adductor muscle scar and pallial sinus.

Remarks. Arcopagia in its broad sense is herein treated as a subgenus, whereas some authors have used it as a full genus, and many workers have divided it into numerous sections. Some traits that typify the group are unstable and liable to alteration among related species; however, the orbicular shape and general thickness of the valves are typical. The lateral dentition is stronger in the right valve than in the left, and the position of these teeth is variable, although the posterior lateral tooth is nearly always distally removed from the cardinal complex. The left lateral dentition is characterized by the obsolescence of the distal posterior tooth and by a variable placement of the anterior tooth. In the type-species, the pallial sinus ascends obliquely and descends to the terminus of the pallial line, so that no confluence occurs; however, the sinus may be confluent with the pallial line for nearly all its length in other species.

Many of the so-called genera delineated in the synonymy have been established on characteristics of trivial or specific significance. Species such as *Tellina victoriae* Gatliff and Gabriel, the type of *Pseudarcopagia*, and *T. disculus* Deshayes of *Zearcopagia* are so closely related to one another, and in turn to *T. ponsonbyi*, that it is difficult to see how anyone could have justified a 'generic' difference. Although the placement of the pallial sinus in these species differs from that in *T. crassa* Pennant, the type of *Arcopagia*, the existence of many species with an intermediate or medially confluent pallial sinus and pallial line indicates the relationship between these geographically separated lineages. The relative strength of the concentric or radial sculpture is likewise an unsatisfactory basis for generic distinction in *Arcopagia*, since many of the forms show a reduction in the strength of the sculpture ontogenetically. *Scutarcopagia* is unique in its rasplike sculpture, but it may be compared to *T. rastellum* and its congeners in *Tellinella*, a species-complex which is consubgeneric with *T. virgata*. One might be inclined to treat *Scutarcopagia* separately, if a genuine radiation of species existed but, as it is, only two forms could be relegated to it: *T. scobinata* and *T. elizabethae* Pilsbry 1917. *Pinguitellina* may constitute a natural group—the type-species being distinct and a number of forms being obviously related. Yet the sculpture is rather strongly concentric in youthful stages and is subsequently worn down to give the smooth appearance of the adult. The pallial sinus, which in *T. robusta* extends near to the anterior adductor muscle scar and then parallels the pallial line for much of its length before becoming confluent for a short distance posteriorly, is widely variable in closely allied species, the confluence often being extensive. The fossil groups *Arcopagiopsis*,

Cyclotellina, and particularly *Arcopagella* Meek, are tentatively placed here, since their relationship to the lineage of the Recent *Arcopagia* is not positively discerned.

Arcopagia is found in the Cretaceous (Stoliczka, 1870). Many species have been described in Cenozoic deposits, and it is well represented in the Eocene of the Paris Basin. In the Recent fauna, the group is most highly developed in the Indo-Pacific. Most species prefer a tropical habitat in rather coarse substrates, but some have cool temperate or even boreal distributions.

Tellina (*Arcopagia*) *ponsonbyi* Sowerby
Plate 6, figures 1–3; Plate 14, figure 1.

Tellina ponsonbyi Sowerby 1889, Jour. Conch., 6: 155, pl. 3, fig. 1 (type-locality not given, 'South Africa' on original label, here designated, Port Alfred, Republic of South Africa; holotype and three paratypes, BMNH 89.4.14.2904–2908).

Tellina rietensis Turton 1932. The marine shells of Port Alfred, South Africa, p. 248, pl. 66, no. 1747 (type-locality, Port Alfred, Republic of South Africa; holotype, Oxford University Museum).

Tellina kraussi Turton 1932. The marine shells of Port Alfred, South Africa, p. 248, pl. 66, no. 1748 (type-locality, Port Alfred, Republic of South Africa; syntypes, Oxford University Museum).

Description. Shell extending to 34 mm in length and to 28 mm in height, irregularly subovate to subtrigonal in outline, inequilateral, equivalve, solid, moderately inflated, with both valves of equal convexity and without a noticeable flexure to the right posteriorly. Umbos subcentral or a little before middle in subtrigonal specimens, not elevated, somewhat pointed and orthogyrous. Anterior margin broadly rounded and convex; ventral margin convex and rising gently posteriorly; anterior dorsal margin short, rather sharply descending and straight to slightly convex or concave; posterior dorsal margin long, irregularly convex, and rather steeply descending; posterior margin not well defined, short, irregularly convex. (In subovate individuals the posterior dorsal margin and posterior margin are not distinguished at all; rather there is an irregularly convex outline to the posterior portions of the shell.) Sculpture consisting of concentric lirations (about 4–7 per mm on central disc) and of radial riblets (about 6–10 per mm on central disc) forming definite reticulate pattern. Concentric growth lines coincident with crowding of concentric lirations present and probably indicative of annual growth—six growth lines in individuals at 2.5 cm and often associated with color differences. Small distinct central portion of ligament subtending umbos. Weak radial ridge emanating from umbo and convexly paralleling posterior dorsal margin posteriorly.

Ligament yellow to brown, elongate, strong, not protuberant, sunken in poorly defined escutcheon; calcareous portion of ligament short, triangular, about 1/2 length of horny portion. No true lunule developed. Hinge line strongly developed. In left valve, cardinal complex consisting of anterior narrowly subdeltoid, bifid cardinal tooth with subequal lobes, and of posterior obsolete elongate cardinal tooth coalesced with internal ligamental element; anterior and posterior lateral teeth strong and pointed, not socketed above; anterior tooth closer to cardinal complex; posterior lateral tooth distal, well beyond end of ligament. In right valve, cardinal complex consisting of weakly bilobed posterior cardinal and obsolete anterior cardinal, often lost or consisting of irregular wrinkle on cardinal plate; anterior and posterior lateral teeth strong, pointed, socketed above; anterior tooth closer to cardinal complex and posterior tooth distal. Distinct groove coextensive with socket above posterior tooth extending length of external ligament.

Muscle scars moderately impressed. Anterior scar irregularly semilunate and posterior subrectangular. Pallial sinus more or less equal in opposite valves, gently rising, sometimes pointed dorsally, rounded anteriorly and coalescent with pallial line for about 1/3 its ventral length posteriorly. Pallial sinus widely separated from the anterior adductor muscle scar. Cruciform

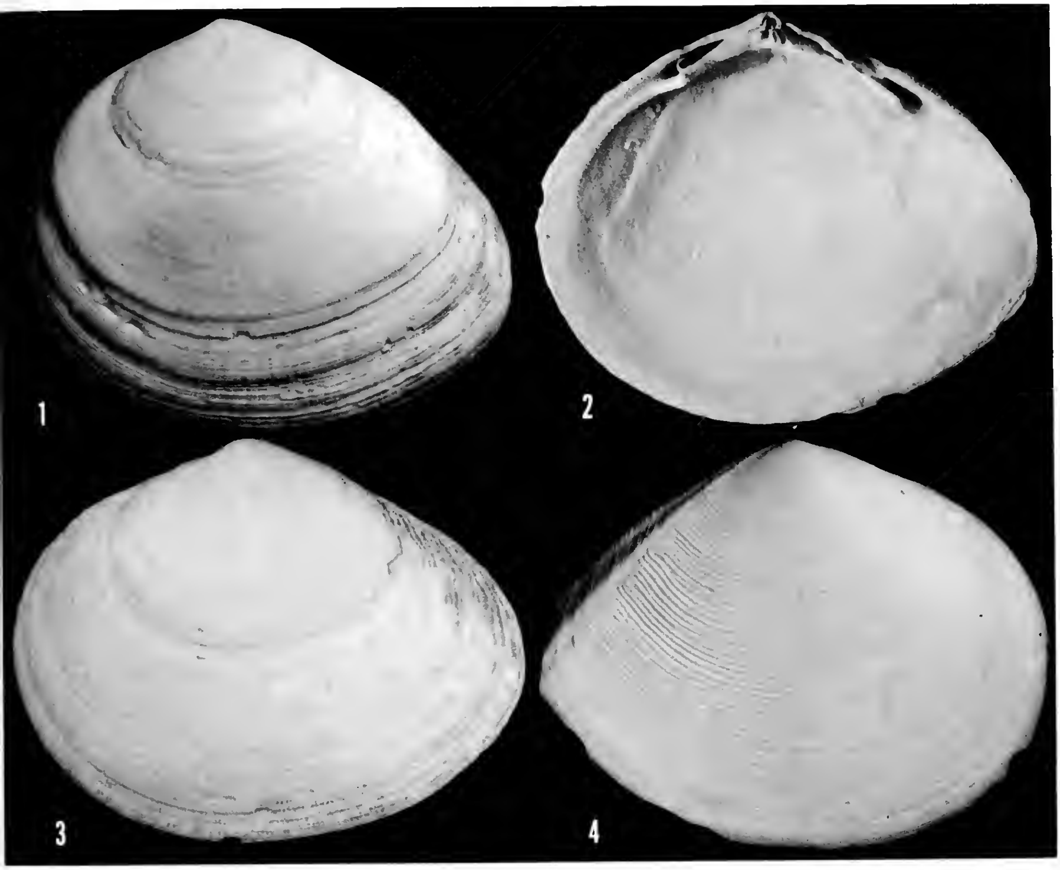

Plate 6. Figs. 1, 2, and 3. *Tellina (Arcopagia) ponsonbyi* Sowerby: Fig. 1, external view of the left valve, Albany, South Africa, USNM 98045 (length = 22.9 mm); Fig. 2, internal view of the right valve, Still Bay, South Africa, SAM A30022 (length = 17.9 mm); Fig. 3, external view of the left valve, Still Bay, South Africa, SAM A30022 (length = 23.9 mm). Fig. 4. *Tellina (Serratina) capsoides* Lamarck: adult individual, external view of the right valve, Durban, NM (length = 57.3 mm).

muscle scars rather distinct, posterior scar larger and set somewhat outward, toward posteroventral margin. Shell white to dirty off-white; internally polished, externally dull with darker concentric growth rings.

Length mm	Height mm	Width mm	
33.5	28.0	12.5	Port Alfred
32.7	26.8	12.7	Algoa Bay
29.0	25.0	12.6	Jeffrey's Bay
25.0	20.0	—	holotype of *ponsonbyi*
22.2	19.4	09.7	Durban
16.0	12.0	—	holotype of *rietensis*
15.0	13.0	—	syntype of *kraussi*
13.8	11.4	06.5	off Tugela River
10.2	08.9	—	Still Bay
03.7	02.8	—	Port Alfred

Remarks. Tellina ponsonbyi is distinguished from other South African tellens by its distinctly cancellate or reticulate sculpture. The concentric portions of the sculpture are strongest peripherally and along the posterior dorsal slope, where they may even become somewhat sublamellate. The synonyms *Tellina rietensis* and *T. kraussi*, introduced by Turton, were based on shape and on beach-worn material, respectively.

As has been indicated in the description, *T. ponsonbyi* undergoes considerable change of shape during ontogeny. Immature

specimens up to 5 mm in length are subquadrate or subrectangular in outline. Gradually they assume the typically subovate to subtrigonal outline of adult specimens. The distinctive sculpture begins to develop when the shell is about 3.5 mm in length. Internally, the dentition and configuration of the pallial sinus are diagnostic.

Specimens of *T. ponsonbyi* could possibly be confounded with *Gastrana abildgaardiana* (Spengler), since the species bear a superficial resemblance to each other. The latter, however, has distinctly stronger concentric sculpture, lacks lateral dentition, and possesses extremely well-developed cardinal teeth—particularly the extremely strong, bilobed, protuberant anterior cardinal in the left valve.

T. ponsonbyi conforms to the morphological patterns seen in *Arcopagia*. The type-species of this group is the European species, *T. crassa* Pennant. The main features that distinguish this subgenus are the presence of well-developed lateral teeth, particularly in the right valve, where the anterior lateral tooth is a little more closely placed in relation to the cardinal complex than is the posterior lateral tooth, and the more or less basically rounded or subovate shape of the valves. A number of other superspecific taxa conform to this generalized pattern and have been established on criteria that cannot be construed as being of subgeneric, much less generic, importance; these are included in the synonymy of *Arcopagia*. In point of fact, these nominal superspecific taxa cloud the true phylogenetic relations of the representative species.

T. victoriae Gatliff and Gabriel 1914 (= *T. decussata* Lamarck 1818, *non* Wood 1815), of New South Wales and South Australia, is a near relative of *T. ponsonbyi*. The pattern again singles out the relationships between the Australian and South African faunas. *T. victoriae* is more nearly perfectly rounded, larger in size (adults longer than 50 mm), and has stronger concentric sculpture than does *T. ponsonbyi*. Further, the pallial sinus in *T. victoriae* is more extensively coalescent with the pallial line. The New Zealand analog is *T. disculus* Deshayes 1854, which has been referred to *Zearcopagia*. The roundly inflated *T. hirasei* Pilsbry 1904 is a Japanese relative of *ponsonbyi*.

Range. *Tellina ponsonbyi* lives in southeast African waters from Still Bay in Cape Province to Zululand; it prefers offshore waters of depths to 95 m. Boshoff (1965) has recorded what he called '*ponsonbyi*' as far north on the eastern coast as Inhaca, Mozambique, where he took a recently dead specimen from under coral talus. The specimen identified by Boshoff is definitely not *T. ponsonbyi* but another Indo-Pacific species, probably *T. fimbriata* Hanley.

Specimens examined. REPUBLIC OF SOUTH AFRICA: Still Bay (SAM); Mossel Bay (UCT); Jeffrey's Bay (MCZ; USNM); Port Elizabeth (BMNH); Algoa Bay (NM; SAM); Albany District (USNM); Port Alfred (BMNH; MCZ; USNM); Port Alfred, near Grahamstown (USNM); Durban (DM; NM); off Tugela River (SAM); off O'Neill Peak, Zululand (SAM).

Tellina (Arcopagia) yemenensis (Melvill)
Plate 7, figures 3, 4; Plate 17, figures 5, 6.

Tellina (*Angulus*) *yemenensis* Melvill 1898, Ann. Mag. Nat. Hist., (7) 1: 203, pl. 12, fig. 11 (type-locality, Aden; holotype, BMNH 98.3.17.6).

Tellina siebenrocki Sturany 1901, Denkschrift. Kaiser. Akad. Wiss., Math.-Naturw. Class, Wien, 69: 278–9, pl. 6, figs. 4–7 (type-locality, Ghulejfaka, Landzunge Ras Medjamila [14°35′N, 74°58′E, Yemen Coast, Red Sea]; holotype, ? Vienna Mus.).

Tellina (*Arcopagia*) *bertini* (Jousseaume MS) Lamy 1918, Bull. Mus. Natl. Hist. Nat. Paris, 24: 120 (type-locality, Aden, Djibouti; holotype, ? MNHNP).

Description. Shell extending to 18 mm in length and to 13 mm in height, subtrigonal, inequilateral, equivalve, rather solid, inflated with short, rather sharp posterior flexure to right. Umbo slightly behind middle, opisthogyrous, elevated,

Plate 7. Figs. 1 and 2. *Tellina (Quidnipagus) palatam* Iredale 1929, Bweju, Zanzibar, USNM 604319: Fig. 1, external view of the right valve (length = 79 mm); Fig. 2, external view of the left valve of an immature individual (length = 9.7 mm). Figs. 3 and 4. *Tellina (Arcopagia) yemenensis* Melvill, Durban Bay, DM (length = 15.6 mm); Fig. 3, external view of the right valve; Fig. 4, internal view of the right valve.

and somewhat blunt; umbonal cavity shallow. Anterior margin smoothly and usually narrowly rounded; ventral margin gently convex, rising in subsigmoid arcuation posteriorly; anterior dorsal margin rather steeply descending, long, and straight to weakly convex; posterior dorsal margin steeply descending, straight, and long; posterior margin short, blunt, irregularly convex, and forming subrostrate outline to posterior aspect of valve. Sculpture consisting of weakly incised, very closely spaced lirations (10–15 per mm), most evident peripherally; centrally smooth; no true radial sculpture. Radial posterior ridges in each valve with weakly depressed sulcal area in front of ridges.

Ligament brownish, protuberant, short, subtended by short, flattened nymphs. No true lunule; escutcheon short, broadly lanceolate; posterior ridges forming broad, flattened, posterior dorsal surface. Hinge line moderately well developed. In left valve, cardinal complex of anterior, subdeltoid to somewhat bifid tooth with more or less equal lobes, and of posterior long, thin, oblique laminate tooth; anterior lateral tooth moderately developed, consisting of thickening hinge line; rather distal to cardinal complex; posterior lateral tooth distal to cardinal complex, weakly pointed. In right valve, cardinal complex consisting of posterior, rather weak, slightly skewed bifid tooth, and of anterior, single, strong,

subdeltoid tooth; posterior lateral tooth distal, slightly upcurled, pointed, and socketed above; anterior lateral tooth very strong, subproximal, upcurled and socketed above. No true internal rib; weakly radially vermiculate.

Muscle scars moderately impressed. Anterior adductor muscle scar irregularly semilunate; posterior adductor muscle scar subelliptical. Pallial sinus rising very steeply posteriorly, arched beneath umbo, falling in straight to subconcave arcuation anteriorly, not confluent with anterior adductor muscle scar and uniting with pallial line just ventral to it. Cruciform muscle scars small, round in left valve; anteriormost in right valve subrectangular, close to periphery. Shell usually flesh colored externally and internally, rarely white or pinkish; sometimes with iridescent sheen.

Length mm	Height mm	Width mm	
17.2	12.6	07.2	Durban Bay
16.5	11.5	06.7	Durban Bay
15.6	11.1	05.7	Durban Bay
12.2	08.2	04.4	Durban Bay

Remarks. Tellina yemenensis is typified by its rather sturdy, solid shell and its thickened dentition in the right valve. The apricot-flesh coloration and the smooth external sculpture are helpful in the recognition of this species. It is variable in color, with the apricot sometimes reduced to a pale yellow-white, though the coloration may be intense and the suffusion complete. Also, all specimens are not so definitively subrostrate posteriorly. The fine illustrations of Sturany (1901) show the typical posterior outline and the form of the pallial sinus.

Salisbury (1934) remarked that he thought *T. yemenensis* belonged to the *T. rutila* Dunker complex; however, the *rutila* group possesses the anguloid facies and is discussed under *canonica* (*q.v.*). Lamy (1918) placed the synonyms of *T. yemenensis* in with *Arcopagia*. Heretofore, the small arcopagoids have been placed in *Pinguitellina* Iredale, with *T. robusta* Hanley as type. Although some authors have employed this name at the generic level (Dall, Bartsch, and Rehder, 1938), *Pinguitellina* represents nothing more than a variation on an arcopagoid theme, which accounts for its appearance in the synonymy of *Arcopagia*. Having a sturdy, rounded, plump shell, *T. yemenensis,* with its strong development of a subproximal right anterior lateral tooth and a distal posterior lateral tooth, is certainly referable to *Arcopagia.*

Tomlin (1926) was the first to report *T. yemenensis* from South Africa, on a single specimen collected at Durban by a Mr. Falcon and preserved in the collection of the Natal Museum (no. 3649). Barnard (1964b), without seeing the specimen, incorrectly referred Tomlin's record to *H. ludwigii.* A number of other specimens have been taken in Durban Bay and, therefore, *T. yemenensis,* though relatively rare, occurs in the area.

Range. This species lives in the Red Sea and in the Indian Ocean from Aden to Durban, South Africa.

Specimens examined. REPUBLIC OF SOUTH AFRICA: Richards Bay, Zululand (UCT); Durban Bay (DM; NM). ADEN PROTECTORATE: Aden (BMNH).

Subgenus *Quidnipagus* Iredale

Quidnipagus Iredale 1929, Mem. Queensland Mus., 9: 266 (type-species, *Cochlea palatam* Martyn 1784 [not available] [= *Tellina palatam* Iredale 1929], original designation).

Description. Shell of medium length, ovate-subtrigonal, solid, inequivalve with right valve of greater convexity and flexed to right posteriorly. Umbos subcentral. Concentric sculpture consisting of lamellate undulations. Dentition well developed; right lateral teeth strong, anterior subproximal to cardinal complex. Pallial sinus extending nearly to anterior adductor muscle scar, broadly rounded, paralleling pallial line ventrally and confluent for posterior half of pallial line.

Remarks. Quidnipagus has hitherto been

considered a section of *Quadrans* (Thiele, 1935). Its relationship to both *Arcopagia* and *Serratina* is indicated by its general ovate shape and its developed right lateral dentition. However, the sculpture is exceptional and the group is evidently monotypic. The so-called *Scutarcopagia* (herein considered as a variation of the arcopagoid theme), including such species as *T. scobinata,* and the *rastellum*-group of *Tellinella,* approach in their scalelike or rasplike sculptures, respectively, the irregular undulations of *Quidnipagus.*

Tellina (*Quidnipagus*) *palatam* (Iredale)
Plate 7, figure 1, 2.

Tellina rugosa Born 1778, Index rerum naturalium Musei Caesarei Vindobonensis, pt. 1, Testacea, p. 18; 1780, Testacea Musei Caesarei Vindobonensis, p. 29, pl. 2, figs. 3, 4 (type-locality, not given; holotype, Vienna [see Brauer, 1878]), *non* Pennant 1777, *nec* Solander 1786, *nec* Römer 1836.

Cochlea palatam Martyn 1784, Univ. Conch., vol. 4, pl. 138 (type-locality, China; types, not known).[1]

Tellina (*Tellinella*) *rugosa obtusa* (Jousseaume MS) Lamy 1918, Bull. Mus. Natl. Hist. Nat. Paris, 24: 29 (type-locality, Red Sea; holotype, MNHNP), *non* Sowerby 1868.

Quidnipagus palatam Iredale 1929, Mem. Queensland Mus., 9: 266 (refers to *Cochlea palatam* Martyn 1787 [1784], Univ. Conch., vol. 4, pl. 138).

Description. Shell extending to 68 mm in length and 53 mm in height, ovate-subtrigonal, subequilateral, inequivalve, solid, somewhat inflated, with right valve of greater convexity, and with sharp and well-developed flexure to right posteriorly. Umbo subcentral, slightly in front of middle, pointed, slightly inflated and smooth. Anterior margin broadly and smoothly rounded; ventral margin gently convex, rounded anteriorly, rising in subconcave postbasal arcuation posteriorly; anterior dorsal margin convex, rounded and gently descending; posterior dorsal margin more steeply descending and more or less straight; posterior margin irregular, straight to slightly convex, forming oblique truncation. Sculpture consisting of concentric irregularly undulate raised lamellations (about 1 per mm) on central disc, becoming stronger on right posterior slope; extremely fine concentric lirations in sulci between lamellations. Extremely fine radial lirations also present in interlamellar sulci; weaker peripherally, most evident umbonally. Single strong posterior radial ridge in right valve and concomitant shallow sulcus in left valve.

Ligament brownish black, strong, slightly protuberant, somewhat sunken in elongate lanceolate escutcheon; lunule elongate, narrow, depressed, stronger in left valve. Calcareous portion of ligament set upon moderately developed and slightly raised nymphal callosities. Hinge line well developed. In left valve, cardinal complex consisting of anterior, very strong, protuberant, deltoid, bifid cardinal tooth with subequal lobes, and of posterior elongate, thin, laminate tooth adpressed to base of nymphal callosity; anterior lateral tooth closer to cardinal complex than posterior, consisting of generalized thickening of hinge line; posterior tooth at posterior end of hinge plate, and escutcheon, thickened and bluntly pointed. In right valve, cardinal complex consisting of posterior narrow bifid tooth with equal lobes and of anterior subdeltoid tooth; anterior and posterior lateral teeth strong, thin, laminate, pointed, slightly upcurled, and socketed above; anterior tooth closer to cardinal complex.

Muscle scars moderately well impressed. Anterior adductor muscle scar subsemilunate, rounded ventrally, with dorsal extension representing anterior pedal retractor scar; posterior adductor muscle scar rounded to subquadrate, with ventral digitiform extension. Pallial sinus more or less equal in opposite valves, rising gently posteriorly, irregularly convex above, falling in smoothly rounded convex arcuation

[1] This work is not available for nomenclatorial purposes. It has been suppressed by the ICZN, Opinion 456.

anteriorly, paralleling pallial sinus for some distance before becoming confluent with it; confluence approximately 1/2 of total ventral length of pallial line; anteriormost extension of pallial sinus close to but not confluent with anterior adductor muscle scar. Cruciform muscle scars rounded, usually conspicuous, large and closely juxtaposed. Externally, shell basically white with some suffusions of yellow umbonally; internally white, sometimes with considerable concentrations of yellow; rarely apricot or pinkish.

Length mm	Height mm	Width mm	
72.0	64.0	25.0	Inhaca, Mozambique
67.4	52.2	25.5	Pukoo, Molokai, Hawaiian Ids.
65.9	52.5	—	Tanapag Harbor, Saipan, Mariana Ids.
46.4	34.9	15.0	Onotoa Atoll, Gilbert Ids.
45.5	34.8	16.2	Bweju, Zanzibar
33.6	24.7	11.3	Bweju, Zanzibar
22.8	17.1	08.2	Bweju, Zanzibar
09.6	07.6	03.5	Bweju, Zanzibar

Remarks. Tellina palatam is primarily characterized by its peculiar undulate sculpture, which causes the surface of the valves to be roughened and sometimes rasplike. In this regard it may be compared to *T. scobinata* Linnaeus, which is clearly arcopagoid and disc-shaped; the sculpture in *scobinata* is formed by small semicircular flanges, its surface being more strongly rasplike than that of *T. palatam*. Likewise, the complex in *Tellinella* represented by such species as *T. rastellum* (*q.v.*) has rasplike sculpture, but it is not uniquely undulate. *T. linguafelis* Linnaeus is a closer relative with a similar but not as strong sculpture. Further, it is of slightly lower proportions and is not as inflated as *T. palatam*. It also is rayed, and its umbo is usually colored reddish.

In *T. palatam* there is some variation in the strength of the sculpture and in the degree of undulation. But the shape of the shell, particularly the extent of pointedness of the posterior slope, is much more variable. Some specimens are very much rounded or shortened behind, whereas others are more distinctly pointed and subtrigonal in outline. The species is noticeably inequivalve, with the right valve more convex, larger, and slightly overlapping the left. The usual basic color pattern is an internal, centrally concentrated, suffusion of yellow. Very infrequently, valves may have pink, orange, or apricot suffusions.

An allometric growth pattern is evident in the ontogeny of the species and has been graphically illustrated by Rost and Soot-Ryen (1955). Smaller individuals tend to be higher and more subquadrate than larger ones.

Range. T. palatam is a relatively common, widely distributed Indo-Pacific species. It is found along the East African coast south to Durban, throughout the Indian Ocean, Indonesia, the Philippine Islands, north to Mogi, Japan, east to the Hawaiian Islands in the north and to the Tuamotus in the south. The species lives in rather shallow water in coarse substrates. It has been found in the Pleistocene of French Somalia (Abrard, 1942), and Skarlato (1965) presented a map of its range.

Specimens examined. REPUBLIC OF SOUTH AFRICA: Durban Bay (NM); Natal (DM; NM). MOZAMBIQUE: Inhaca (Boshoff). TANZANIA: Dar-es-Salaam (ANSP; BMNH; USNM); Mboa Maji, 9 mi. S of Dar-es-Salaam (USNM); Leopard's Cove at Msasani (MCZ); 1.5 mi. NW of Magogoni (MCZ); fringe rock and sand, in 0–5 ft. (1.5 m), Dembiani, 2 mi. N of Kizimkazi, Zanzibar (ANSP; MCZ); Kiwengwa, 18 mi. N of Chwaka, Zanzibar (USNM); Bweju, Zanzibar (USNM); Mbweni, 4 mi. S of Zanzibar City (USNM); Uroa, Zanzibar (USNM); sand and reef, in 0–10 ft. (3 m), 1 mi. N of Paje, Zanzibar (ANSP); Kijangwami, Zanzibar (USNM); sand, grass and coral rock, in 0–4 ft. (1.2 m), Chwaka, Zanzibar (ANSP). KENYA: Mombasa Id. (ANSP); Malindi, 76 mi. N of Mombasa (USNM). FRENCH SOMALILAND: Djibouti (ANSP). RED SEA: (BMNH; MCZ). ETHIOPIA: Massawa, Eritrea

(MCZ). SUDAN: Port Sudan (ANSP). ISRAEL: Akaba (MCZ). ADEN PROTECTORATE: Aden (BMNH). MADAGASCAR: W of Sangeritela, 9 mi. NNW of Tuléar (MCZ); Faty (Ifatz), 13 mi. N of Tuléar (MCZ); shallows of beach, W of Marosoroka, 2.5 mi. N of Ambodifototra, Ile Ste. Marie (MCZ); Nossi Bé (MCZ); in 0–12 ft. (3.7 m), sand, grass, rock, coral, inside crater, Pte. du Cratere, SW Nossi Bé (dead) (ANSP); 0–10 ft. (3 m), muddy, sand ledge, rock, coral, W of Pte. de Tafondro, SE Nossi Bé (ANSP); 0–8 ft. (2.4 m), sand, rock, coral, Nosy Tanikely, 4 mi. S of Nossi Bé (ANSP). SEYCHELLES IDS.: (BMNH; MCZ); NW Bay, Mahé (BMNH). MAURITIUS: (MCZ); 0-10 ft. (3 m), sand, weed, rock and coral, Flic en Flacq (ANSP); Pt. d'Espy (ANSP); near Port Louis (MCZ); 0–12 ft. (3.7 m), sand flat, fine grass, sponge, Jerome Pt., 1 mi. SE Mahebourg (ANSP); 0–4 ft. (1.2 m), sand and weed, around rock point, 1/4 mi. SW Cap Malheureux (ANSP). MALDIVE IDS.: 150–210 ft. (32–64 m), E of Kohit Lowalafuri, NW of Maduwarils, Fadiffolu Atoll (ANSP); NW tip of Gan, Addu Atoll (ANSP). NICOBAR IDS.: (BMNH). COCOS-KEELING IDS.: 1–2 ft. (0.3–0.6 m), *Thalassia,* mixed *Caulerpa* and some corallines, few dead corals, lagoon, E side S end of West Id. (ANSP). THAILAND: coral reef and sand lagoon, Aokam, S end of Phuket Id. (ANSP); sand, live coral, basalt shore, Laam Phan Wa, Phuket Id. (ANSP); Kok Tao, Gulf of Siam (USNM). INDONESIA: Bay of Batavia, Java (USNM); Tjiperwagaran, Bantam, Java (USNM); Keleditan, Bantam, Java (USNM); Oedjoeng Genteng, SW Java (MCZ); Koeta Beach, Bali (MCZ); Biak Id., Schouten Ids. (USNM); Aitape, New Guinea (MCZ). CHINA: Sanya, Hainan (ANSP). JAPAN: Mogi (USNM); Ryukyu Ids. (ANSP; BMNH; MCZ; USNM); Homan, Okinawa (ANSP); Shioyas, Skanawan Bay, Okinawa (USNM); Abu, Okinawa (USNM); beach at Kanna, Okinawa (MCZ). PHILIPPINE IDS.: shore reef, Cape Santiago, Batangas, Luzon (ANSP); Masinloc Bay, Zambales, Luzon (USNM); Barrio-Lupi, Prieto Diaz, Sorsogon, Luzon (ANSP); E coast of Polillo Id. (USNM); Gigmoto, Catanduanes Id. (ANSP); Lubang Id. (USNM); Malug, Lubang (MCZ); Tilic Beach, Lubang (MCZ); Cabila, Barrio of Tagbac, Lubang (MCZ); Calapan, Mindoro (MCZ); Cabra Id. (MCZ); Busuanga, Calamian Group (USNM); Palawan (MCZ); Cuyo Cuyo Group (MCZ); Cagayancillo (USNM); Loran Id., Ubian (USNM); Tataan Id., Tawi Tawi Group (USNM); Bongao Channel, SW end Sanga Sanga Id., Sulu Archipelago (ANSP); Negros (USNM); Cebu City, Cebu (ANSP); Mantacao Id., Bohol (USNM; Zamboanga, Mindanao (ANSP); Little Santa Cruz Id. (USNM); Lianga Bay, Mindanao (USNM); Basilan (USNM). AUSTRALIA: Dunk Id., Queensland (ANSP); Innaminca Point, Queensland (ANSP). PALAU IDS.: Kayangel Id., Kayangel Atoll (USNM). MARIANA IDS.: Unai Fanunchuluyan, Saipan (USNM); Tanapag Harbor, Saipan (ANSP; USNM); Chalan, Kanoa, Saipan (MCZ); Agana Bay, Guam (ANSP); Apra Harbor, Guam (ANSP); Piti Bay, Guam (MCZ); Merizo, Guam (MCZ). CAROLINE IDS.: Ulithi (USNM); Yin, Yap (USNM); Tomil Harbor, Yap; Balabat, Yap (tide flats) (USNM); Ponape (ANSP). MARSHALL IDS.: Wotho Id., Wotho Atoll (USNM); Lea Atoll (USNM). GILBERT IDS.: Makin Id. (USNM); Onotoa Atoll (MCZ); S 50 W from Tekawa Church, at seaward edge of Aonte Baba reef, Onotoe Atoll (USNM); Apaiang (MCZ). BISMARCK ARCHIPELAGO: Kumbun Id., SW New Britain Id. (ANSP). NEW CALEDONIA: (BMNH; MCZ; USNM); Tonghoue, 45 mi. N. of Noumea (ANSP); Bourail (ANSP); Gatope Id., Voh (ANSP); Koë Reef, 2 mi. SSE Touho (ANSP). FIJI IDS.: (BMNH); between Port Ellington and Korokala, NE Viti Levu (USNM); near Port Ellington Wharf, Point Ellington,

5 mi. E of Rakiraki, NE Viti Levu (MCZ); Fring Reef, Lorolevu, Viti Levu (ANSP); Suva, Viti Levu (USNM); Nandronga, Viti Levu (USNM); Mbenga (MCZ); shore reef, 1/2 mi. N of Tunuloa, Vanua Levu (MCZ); Thithia Id., Lau Group (USNM); Mothe Id., Lau Group (USNM). SAMOA IDS.: (USNM); Upolu Id. (ANSP; MCZ; USNM); Massacre Bay, Tutuila Id. (MCZ; USNM). COOK IDS.: E side of Akitua, NE Aitutaki (ANSP); W side Akitua, NE Aitutaki, in 0–2 ft. (MCZ); N Puapuautu, SW of Motutua Id., NW Rarotonga (ANSP); Mangaia (USNM). SOCIETY IDS.: Faanui, Borabora (ANSP); Bora Bora (ANSP); Raiatea (ANSP); Huahine Id. (ANSP); Tahiti (MCZ; USNM); Atiue, Punaauia, Tahiti (ANSP); Tupai Id., Motu-iti, Austral Ids. (ANSP); Opara (Rapa) (ANSP). TUAMOTU ARCHIPELAGO: Maranguai Islet, Toau Atoll (ANSP). HAWAIIAN IDS.: Hilo Bay (MCZ); Keokea Bay (USNM); Kainalu, Molokai Id. (ANSP); Kapulei, Molokai Id. (ANSP); Pukoo, Molokai (USNM); Honolulu, Oahu (ANSP); Waikiki, Oahu (ANSP); Pearl Harbor (fossil) (USNM); Hospital Point Beach, Pearl Harbor (USNM); Ford's Id., Pearl Harbor (ANSP); 1.8 mi. E of Pearl City Road (ANSP; MCZ); Mokuoloe Id., Kaneohe Bay (ANSP); Makapu Peninsula, Kaneohe Bay (MCZ; USNM); E of Aiea station (ANSP); Hoaeae (ANSP); Heeia Pond (fossil) (USNM); Kewalo Reef (MCZ; USNM); Sanikai (USNM); 1/2 mi. W of Waipahaehoe station (ANSP); NW corner Weli Pond (fossil) (USNM); Kilauea Beach, Kauai Id. (ANSP).

Subgenus *Serratina* Pallary

Pristis Lamy 1918, Bull. Mus. Hist. Nat. Paris, 24: 29 (type-species, *Tellina pristis* Lamarck 1818, original designation), *non* Linck 1790, Latham 1794, Müller and Henle 1837 (Pisces), *nec* Brullé 1846 (Insecta).

Serratina Pallary 1922, Exploration scientifique du Maroc, Malacologie (1912), p. 95 (type-species, *Tellina serrata* [Renier MS] Brocchi 1814, original designation).

Striotellina Thiele 1935, Handbuch der systematischen Weichtierkunde, vol. 2, pt. 3: 917 (type-species, *Tellina serrata* Renier 1804,[1] monotypy).

Pistris Thiele 1935, Handbuch der systematischen Weichtierkunde, vol. 2, pt. 3: 917, new name for *Pristis* (Jousseaume MS) Lamy 1918, *non* Linck 1790, Latham 1794, Müller and Henle 1837 (Pisces) *nec* Brullé 1846 (Insecta).

Pristipagia Iredale 1936, Rec. Aust. Mus., 19 (5): 281 (type-species, *Pristipagia gemonia* Iredale 1936, here designated).[2]

Lyratellina Olsson 1961, Panamic-Pacific Pelecypoda, p. 383 (type-species, *Tellina lyra* Hanley 1844, original designation).

Description. Shell of small to medium size, somewhat compressed, subovate to subquadrate in shape, nearly equivalve, and more or less equilateral. Umbos rather centrally placed. Sculpture predominately concentric, consisting of more or less closely and regularly spaced lirations, sometimes sublamellate in immature stages. Dentition well developed, with anterior and posterior lateral teeth more or less equidistant from cardinal complex. Pallial sinus larger, extensive, rounded anteriorly, sometimes coextensive with anterior adductor muscle scar or rarely paralleling pallial line and confluent posteriorly. Color predominately white or dull grey.

Remarks. This group is typified by having rather solid, whitish or grayish shells that tend to be irregularly subquadrate in shape and that have a predominately concentric sculpture consisting of more or less regularly spaced, incised sulcations that may be sublamellate posteriorly. The pallial sinus is generally extensive and broadly rounded anteriorly or, in some

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[1] The "Tavola alfabetica delle Conchiglie Adriatiche" of Renier (1804) was suppressed by the ICZN (Opinion 316); the next available usage of *T. serrata* was by Brocchi (1814).

[2] The slovenly work of Iredale! In establishing this 'genus,' he (1) does not designate a type-species, (2) implies a renaming of *Pristis* (Jousseaume MS) Lamy, and (3) mentions *capsoides* Lamarck, *botanica* Hedley, and *gemonia* Iredale. In Iredale and McMichael (1962), the latter is taken as the type-species by original designation; it is herein correctly and subsequently designated as type-species.

cases, coextensive with the anterior adductor muscle scar. The right lateral dentition is developed, and the anterior and posterior lateral teeth are more or less equidistant from the cardinal complex.

T. serrata represents the group in the eastern Atlantic, *T. aequistriata* in the western Atlantic, *T. alerta* in the southern Atlantic, *T. reclusa* in the eastern Pacific, and *T. capsoides* in the Indo-Pacific. The group is closely related to *Quadrans* Bertin, which differs in its smooth surface and peculiarly differentiated subspinose posterior lamellations.

I had earlier (Boss 1966b) placed *T. aequistriata* and *T. alerta*, here considered in *Serratina*, in *Merisca* Dall 1900 with *T. crystallina* Wood 1815 (= *T. cristallina* Spengler 1798) as type-species. This thin fragile species (with a rostrate posterior outline and a right anterior lateral tooth subproximal to the cardinal complex), along with the eastern Pacific *T. rhynchoscuta* Olsson and the Indo-Pacific *T. martensi* Lynge, may be considered as forming a rather distinct lineage related to, but not consubgeneric with, the *Serratina* group.

I have, however, included *Lyratellina* Olsson in this synonymy, which thereby brings such species as *T. martinicensis* d'Orbigny, *T. juttingae* Altena, *T. proclivis* Hertlein and Strong, and *T. lyra* Hanley into the fold of *Serratina*. The sole distinguishing character of *Lyratellina*, the prosogyrous proclivity of the umbos, is really not a constant trait, and the species exhibit a variation through the prosogyrate, orthogyrate, and opisthogyrate conditions.

Tellina (*Serratina*) *capsoides* Lamarck
Plate 6, figure 4; Plate 8, figures 5, 6; Plate 14, figure 3.

Tellina capsoides Lamarck 1818, Anim. sans Vert., 5: 531 (type-locality, à l'île St. Pierre-St.-Francois[1]; types, MNHNP [see Bertin, 1878]); Hanley 1847 [*in*] Sowerby, Thes. Conch., vol. I, *Tellina*, p. 268, pl. 62, fig. 185.

Tellina pristis Lamarck 1818, Anim. sans Vert., 5: 531 (type-locality, l'Ocean Indien; types, MNHNP [see Bertin, 1878]; refers to Bruguière, 1798, Encycl., Méthod., pl. 287, figs. 1a, b).

Tellina lima Philippi 1847, Zeitschr. Malakozool., 4: 74 (type-locality, China, insula Basilan; holotype, ?).

Tellina (*Arcopagia*) *concentrica* Gould 1850, Proc. Boston Soc. Nat. Hist., 3: 253 (type-locality, Feejee [Fiji] Islands; types, unknown [see Johnson, 1964]); 1852, U. S. Exploring Exped., 12: 404, pl. 36, fig. 519 a-b; 1862, Otia Conch., p. 80.

Tellina diaphana Deshayes 1854, Proc. Zool. Soc. London [1855] pt. 22, no. 282: 364 (type-locality, Japan; syntypes, BMNH, unnumbered).

Tellina denticulata Deshayes 1854, Proc. Zool. Soc. London [1855] pt. 22, no. 282: 365 (type-locality not given; syntypes, BMNH, unnumbered).

Tellina (*Areopagia* [*sic*]) *siamensis* von Martens 1860, Proc. Zool. Soc. London, pt. 28 [1]: 18 (type-locality, Siam; syntypes, BMNH 59.5.23.5).

Tellina negrosiensis Bertin 1878, Nouv. Arch. Mus. Hist. Nat. Paris, 2 Sér., 1: 250, pl. 8, figs. 6a-b (type-locality, îles Negros [Philippine Islands]; syntypes, MNHNP).

Tellina (*Tellinella*) *thymares* Melvill 1896, Proc. Malac. Soc. London, 2: 116, pl. 8, fig. 9 (type-locality, Bombay; holotype, BMNH 96.10.162).

Tellina (*Merisca*) *pristiformis* Pilsbry 1901, Proc. Acad. Nat. Sci. Philadelphia, 53: 400, pl. 19, fig. 8 (type-locality, Inland Sea, Japan; syntypes, ANSP 71029).

Pristis audouini (Jousseaume MS) Lamy 1918, Bull. Mus. Natl. Hist. Nat. Paris, 24: 30 (type-locality, Suez; types, MNHNP; refers to Savigny, 1817, pl. 8, fig. 11, 1–3) (see Audouin, 1827; Pallary, 1926).

Tellina (*Pristis*) *pristis major* Lamy 1918, Bull. Mus. Natl. Hist. Nat. Paris, 24: 30 (type-locality, Suez; types, MNHNP).

Description. Shell extending to 59 mm in length and to 47 mm in height, subovate to subtrigonal, nearly equilateral, nearly

[1] No author has pin-pointed this locality. There is a St. Peter's Island near the St. Francis Island Group of the Nuyts or Moyts Archipelago off South Australia (32°17′S; 133°35′ E), and since it is known that Péron and Lesueur collected along this coast (Péron and Lesueur, 1816) and that the type-specimens of *capsoides* were collected by them (Bertin, 1878, p. 250), it is possible that this locality is the one meant by Lamarck. However, *T. capsoides* does not occur in South Australia (Cotton and Godfrey, 1838), and it is presently assumed that the original locality is incorrect.

equivalve, solid, moderately inflated, with right valve slightly more convex and with weak flexure to right posteriorly. Umbo subcentral, sometimes slightly behind middle, somewhat oblate and pointed. Anterior margin broadly, smoothly, and convexly rounded; ventral margin convex, rising arcuately behind; anterior dorsal margin straight to slightly concave, short and gently descending; posterior dorsal margin longer, more steeply descending, and weakly convex; posterior margin short, biangulate, more or less straight, and forming blunt dorsoventral truncation, sculpture various, with concentric lirations (usually 2–4 per mm) and, in immature specimens, becoming lamellate and subspinose along anterior and posterior dorsal margins. Radial sculpture usually weak and incipient, rarely strong, rather regularly and finely spaced, most noticeable in interspaces or sulci between lirations, and forming microscopic cancellate pattern. Double posterior ridge with shallow sulcus in right valve, weaker in left valve.

Ligament dark brown to black, strong, elongate, slightly protuberant, set in elongate, lanceolate escutcheon; lunule lanceolate, generally impressed and sunken, somewhat more extensive in right valve. Calcareous portion of ligament well developed and subtended by slightly raised nymphal callosities. Hinge line strongly developed and thickened. In left valve, cardinal complex consisting of anterior, rather thin, deeply cleft bifid tooth with subequal lobes, and of posterior elongate, variously developed, laminate cardinal tooth; lateral teeth consisting of slightly pointed thickenings of hinge line, posterior somewhat weaker and somewhat more distally removed from cardinal complex. In right valve, cardinal complex consisting of posterior, strong, protuberant, subdeltoid, deeply cleft bifid tooth with elongate lobes, and of anterior, oblique, strong, laminate tooth; lateral teeth strong, bluntly pointed, and socketed above; posterior lateral more distally removed from cardinal complex.

Muscle scars moderately well impressed. Anterior adductor muscle scar irregularly semilunate and large; posterior adductor scar small, rounded to subquadrate and with ventral digitiform extension. Pallial sinus more or less equal in opposite valves, rising sharply from posterior adductor muscle scar, arcuately or slightly pointed above, descending normally in front, paralleling pallial line for some distance before becoming confluent with it; confluence 1/4 to 1/3 length of pallial line. Cruciform muscle scars closely juxtaposed; anterior scar flattened and larger. Color basically dull or powdery white; rarely, extremely pale yellowish suffusions externally, as well as dehiscent grayish periostracum; rarely, faint pinkish suffusion along hinge posteriorly.

Length mm	Height mm	Width mm	
58.0	46.4	22.4	Durban
56.7	46.1	19.6	Congella
49.0	35.0	15.3	Enoshima, Japan
43.9	33.0	15.0	Manila, Luzon, P. I.
32.9	25.2	11.5	Enoshima, Japan
32.2	26.1	10.9	Dar-es-Salaam, Tanzania
28.3	20.4	07.9	Aden
17.1	12.7	04.4	Durban

Remarks. T. capsoides is an extremely variable species, which accounts in part for the numerous synonyms. As variable as it is, the species is always recognized by the presence of its regular concentric sculpture and the strong development of its right lateral teeth, as well as the digitiform process extending ventrally from the posterior adductor muscle scar. Radial sculpture is usually evident in all specimens, but in some it becomes noticeably stronger; Bertin's *negrosiensis* is based on this variation. The exact proportions of the valves that determine the shape or outline of the shell are also variable, some individuals being less rounded than the East African populations. In Japanese populations that have been referred to *diaphana*, the concentric sculpture is rather weak on the anterior dorsal portions of the disc, and the incidence of individuals with a

slightly subtrigonal shape is greater. Melvill's *thymares* appears to have been founded on specimens of *capsoides* that were not as solid or thickly shelled as usual.

There is an ontogenetic difference in the placement and configuration of the pallial sinus. In young individuals the pallial sinus is smoothly and regularly rounded anteriorly and is distinctly separated from the anterior adductor muscle. In larger or adult specimens the anterior adductor muscle scar is larger and the pallial sinus more extensive. The pallial sinus in adults is, therefore, very closely juxtaposed or contiguous with the anterior adductor muscle scar, and its more or less regularly convex arcuation becomes irregular and slightly displaced.

Krauss (1848) noted the occurrence of this species on the Natal coast. In Mozambique it has been recorded by Braga (1956), Paes da Franca (1960b) and Boshoff (1965). The species has a tropical Indo-Pacific form that comes down the east coast of Africa into the Durban area, which is its southernmost range extension. However, the species thrives well in this area. Day and Morgans (1956) found that it prefers soft substrates of sands and muds and lives in the intertidal open bay and sanctuary of Durban, while Macnae and Kalk (1958) noted that it occurs in the upper and lower midlittoral sands of Inhaca. Specimens that are darkly colored externally often come from soft muddy substrates.

A close relative of *T. capsoides* is *T. serrata* Brocchi from the Mediterranean and the eastern Atlantic (Weinkauff, 1867). The latter is of slightly different proportions, being somewhat more subtrigonal and is generally smaller in size; it tends to be shorter and never as heavily shelled as *T. capsoides*. The concentric sculpture of *serrata* is somewhat finer and the anterior lateral tooth of the valve is closer to the cardinal complex.

Range. Tellina capsoides is an Indo-Pacific species that lives along the east coast of Africa as far south as Durban, throughout the Red Sea (Lamy, 1918; Moazzo, 1939), the Indian Ocean, the Philippine Islands, north to Hokkaido, Japan, south to Queensland, Australia, and east to Vanua Levu in the Fiji Islands. Biggs and Grantier (1960) documented its presence in the Persian Gulf.

Specimens examined. REPUBLIC OF SOUTH AFRICA: Durban (NM; SAM); Durban Bay (UCT; USNM); Congella (NM); Natal (BMNH). MOZAMBIQUE: Morrumbene Estuary (UCT); Inhaca Id. (MCZ). TANZANIA: Dar-es-Salaam (USNM); Zanzibar (MCZ); Mazizini, Zanzibar (ANSP); Mnazi Moja, Zanzibar City (USNM). ADEN PROTECTORATE: Aden (BMNH; USNM). MADAGASCAR: Faty (Ifatz), 13 mi. N of Tuléar (MCZ); Mangroves, mud flats and rocks, Ambatozavavy, E of Nossi Bé; 0–2 ft., NW Nossi Bé (both ANSP); Nossi Bé (MCZ). WEST PAKISTAN: Mekran Coast (MCZ); Baba Id., Karachi (BMNH). INDIA: Bandra, N of Bombay (USNM); Darwar, N Kanara (USNM); Madras (BMNH). ANDAMAN IDS.: (BMNH). BURMA: Akyab, Aracan (BMNH). MALAYSIA: Singapore: (ANSP; BMNH; MCZ; USNM); sand bed and shallow river, Kranji, Singapore (ANSP). THAILAND: sand flats, S end Pa Tong Bay, Phuket Id. (ANSP); intertidal mud flat, Ang Hiu, Cholburi Province (MCZ). CHINA: Tsi Mei, Amoy (ANSP); Whampoa, 12 mi. E of Canton (USNM); Hong Kong (USNM); Haik'ou, Kainan (ANSP; USNM). JAPAN: (BMNH; MCZ); Hokkaido (USNM); Tokyo (Jeddo) Bay (ANSP); Yokohama (BMNH; USNM); Tosa (ANSP); Hirado, Hizen (ANSP; USNM); Enoshima (USNM); Mogi (USNM) Otoshima, Bitchu (ANSP; MCZ; USNM); Satsuma (ANSP); Inland Sea (ANSP; MCZ); Ryukyu Ids. (USNM). PHILIPPINE IDS.: E coast of Polillo Id. (USNM); Manila, Luzon (USNM); Matabunkay Cove, 14 km south of Nasugbu, Manila Bay (ANSP);

Tilic Bay, Lubang Id. (MCZ); Marinduque Id. (USNM); Batangas Prov., Luzon (ANSP); Oago, 4 km north of Gubat, Sorsogon, Luzon (ANSP); Calbayog, Samar Id. (MCZ); near Cebu City, Cebu Id. (ANSP; MCZ); Negros Id. (USNM); Bago and Miranda Beach, Pontevedra, Negros (ANSP); Sinay, Mindanao (USNM); Miramis Beach, Mindanao (USNM); Basilan (MCZ). AUSTRALIA: mud and reef, 1 mi. SE of False Cape Bossut, La Grange Bay (ANSP); Buccaneer Rock, Broome (ANSP); Quailsoland, 35 mi. W of Darwin (MCZ); Darwin (MCZ); Port Essington, Coburn Peninsula (BMNH); Rockingham Bay, Queensland (MCZ); Hervey Bay, Queensland (BMNH); Moreton Bay (MCZ). NEW CALEDONIA: (BMNH; MCZ). FIJI IDS.: Suva, Viti Levu (ANSP; MCZ); between Port Ellington and Korokula, NE coast of Viti Levu (USNM); Buca Bay, Vanua Levu (Moutha Bay) (MCZ).

Subgenus *Pharaonella* Lamy

Pharaonella Lamy 1918. Bull. Mus. Natl. Hist. Nat. Paris, 24: 31 (type-species, *Tellina pharaonis* Hanley 1844, by virtual tautonymy).

Description. Shell of medium to large size, thin, subovate to elongate, posteriorly rostrate and slightly flexed to right posteriorly. Umbos rather small, pointed, median or slightly posterior. Smooth, or sculpture weakly developed. Ligament short, rather weak, not too protuberant, somewhat inset. Dentition small and weak; anterior and posterior lateral teeth developed in right valve, thin, shelf-like and pointed. Pallial sinus moderately large, rather pointed anteriorly, low dorsally, confluent with posterior quarter of pallial line. Color white to deep red, variously banded or rayed.

Remarks. The name *Pharaonella* was suggested by Jousseaume in an unpublished manuscript and then introduced by Lamy (1918). The group was not critically circumscribed, but it has been used at the generic level (Dall, Bartsch, and Rehder, 1938). Its major diagnostic characteristics include its rostrate posterior outline and its colorful, relatively smooth, thin shell; the right valve preserves a full complement of lateral dental elements. Since a number of so-called species are referable to *Pharaonella*, I shall deal with them in the remarks and synonymy of *T. perna*.

Pharaonella is related to *Laciolina* Iredale, a group with such members as *T. chloroleuca* Lamarck and *T. quoyi* Sowerby from the Indio-Pacific, *T. laevigata* Linnaeus and *T. magna* Spengler from the western Atlantic, and *T. ochracea* Carpenter from the eastern Pacific (Boss, 1964). *Laciolina* is more thickly shelled, usually rounded in outline and with a strong, inset calcareous ligamental element. Certain species indicate the propinquity of the lineages of these two groups—so much so, that at times, one tends to doubt their existence as distinct subgenera.

Tellina (Pharaonella) perna Spengler
Plate 8, figures 1–4.

Tellina perna Spengler 1798, Skrivter af naturhistorie Selskabet, København, 4(2): 79 (type-locality, Fra Ostindien; holotype, ex museo Moltkiano, ?Zoological Museum, Copenhagen; refers to Chemnitz 1782, Conch.-Cab., vol. 6: 112, pl. 11, fig. 104 [here selected as type-figure]).

Tellina pallescens Dillwyn 1817, Cat. Shells, 1: 84 (type locality, East Indian Seas; refers to Chemnitz 1782, Conch.-Cab., vol. 6: 112, pl. 11, fig. 104 [here selected as type-figure]).

Tellina latirostra Lamarck 1818, Anim. sans Vert., 5: 523 (type-locality, habite . . . les mers de l'Inde; holotype, MHNG).

Tellina sulphurea Lamarck 1818, Anim. sans Vert., 5: 523 (type-locality, habite l'Ocean Indien . . . ; syntypes, MHNG).

Tellina pharaonis Hanley 1844 (Dec.) Proc. Zool. Soc. London, pt. 12, no. 139: 148 (type-locality, Red Sea; type, Museum Metcalfe [not in the BMNH]); 1846 [*in*] Sowerby, Thes. Conch., 1: 235, pl. 63, fig. 215.

Tellina venusta Deshayes 1854, Proc. Zool. Soc. London [1855 (May)], pt. 22, no. 282: 368 (type-locality, Sandwich Islands; holotype, BMNH).

Tellina semilaevis von Martens 1865, Ann. Mag. Nat. Hist., (3) 16: 429 (type-locality, Querimba Islands, near Mossambique, here restricted; holotype, ?Berlin).

Tellina tenuilirata Sowerby 1868 (March) [*in*] Reeve, Conch. Icon., vol. 17, **Tellina**, pl. 43, fig.

253 (type-locality, unknown; ?syntypes, BMNH 77.5.12.75), *non tenuilirata* Sowerby 1867 (Sept.), *ibid.*, pl. 39, fig. 219a-b.

Tellina tenuisulcata Sowerby 1869 (April) [*in*] Reeve, Conch. Icon., vol. 17, **Tellina**, Index, p. 4, new name for *tenuilirata* Sowerby 1868 (March), *ibid.*, pl. 43, fig. 253, *non tenuilirata* Sowerby 1867 (Sept.), *ibid.*, pl. 39, fig. 219 a-b.

Tellina beadleianus Tryon 1869 (May), Amer. Jour. Conch. [1868], 4 (suppl.): 82, new name for *T. tenuilirata* Sowerby 1868, *non* Sowerby 1867.

Description. Shell extending in length to 77 mm and in height to 33 mm, subelliptical, pointed behind, inequilateral, equivalved, fragile or thin in immature stages to subsolid as adults. Valves only slightly inflated, of more or less equal convexity, and with a sharp flexure to the right posteriorly. Umbo slightly behind middle, little elevated, pointed, and rather inconspicuous. Anterior margin rather narrowly rounded; ventral margin broad or gently convex, rising behind in a postbasal arcuation; anterior dorsal margin gently descending, elongate and nearly straight; posterior dorsal margin gently descending, straight to slightly concave and elongate; posterior margin short, bisected by posterior sulcus, and forming blunt oblique posterior truncation. Posterior outline of valves rostrate. Sculpture consisting of weak concentric lirations (about 3–6 per mm); extremely fine radial vermiculations usually developed on posterior dorsal slope of right valve. Two primary posterior ridges in right valve generally moderately developed; anteriormost in posterior third of valve radiating from umbo to ventral margin; posteriormost in posterior eighth of valve radiating from umbo to junction of posterior margin and ventral margin. In left valve, ridges not nearly as well developed as in right valve.

Ligament yellow to dark brown in color, moderately strong, not protuberant, and set in narrowly lanceolate escutcheon; weak semi-lanceolate lunule present in left valve; calcareous portion of ligament well developed, subtended by hinge margin; no developed nymphal callosities. Hinge line rather moderately developed. In left valve, cardinal complex consisting of interior subdeltoid, bifid tooth with subequal lobes, and of posterior elongate, laminate tooth, slightly thickened or lost; no true anterior lateral tooth, but anterior margin slightly thickened distally; posterior lateral tooth distal, consisting of weak, slightly pointed or thickened tubercle at posterior end of hinge margin. In right valve, cardinal complex consisting of posterior, narrow, bifid tooth with subequal lobes and of weakly subdeltoid or thickened anterior laminate tooth; anterior lateral tooth concave or socketed above, slightly upcurled, and pointed; posterior lateral tooth socketed above, weaker, consisting of pointed, shelf-like extension of hinge margin. No true internal rib, but in right valve, posterior sulcus forming slightly rib-like structure internally.

Muscle scars moderately well impressed. Anterior adductor muscle scar irregularly semilunate and rounded below; posterior adductor muscle scar irregularly rectangular. Pallial sinus equal in both valves, arising from the base of the posterior adductor muscle scar in gentle arcuation, rounded or somewhat pointed above, gently descending anteriorly, forming pointed arcuation anteriorly, and united with pallial line basally for at least one half of its length. Cruciform muscle scars moderately well impressed, subequal in each valve, strongest in right; posterior cruciform scar in right valve on sulcal rib. Color basically white; yellow suffusions usual; umbo occasionally red; infrequent reds and pinks variously distributed in bands or rays.

Length mm	Height mm	Width mm	
76.2	32.9	11.8	Midway Island
66.3	33.3	14.7	Durban
53.0	23.0	08.5	Natal
37.8	19.6	07.4	Java
31.1	13.3	05.0	Durban
22.6	11.4	04.5	Durban

Remarks. Tellina perna Spengler exhibits considerable variation in conchological traits and has a very extensive

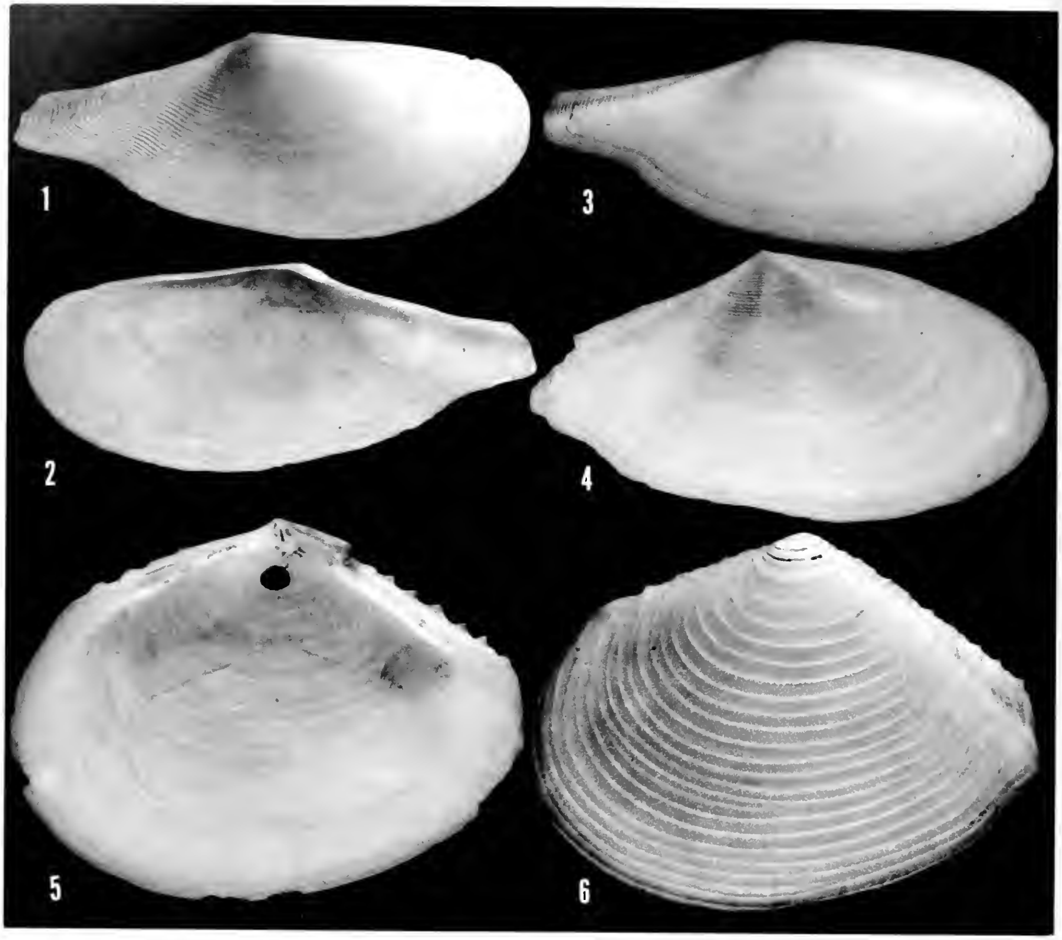


Plate 8. Figs. 1–4. *Tellina (Pharaonella) perna* Spengler: Fig. 1, external view of the right valve, showing extreme development of concentric lirations, Durban, NM (length = 45 mm); Fig. 2, internal view of the right valve, Durban, NM (length = 45 mm); Fig. 3, external view of the right valve, showing normal concentric sculpture, Durban, A3655 (length = 44.5 mm); Fig. 4, external view of the right valve, showing variation in height, Durban Bluff, NM 1775 (length = 20.5 mm). Figs. 5 and 6. *Tellina (Serratina) capsoides* Lamarck, young individual, Durban, NM 3650 (length = 17 mm): Fig. 5, internal view of the right valve; Fig. 6, external view of the left valve.

geographical range. The species is highly variable, with certain of its widely dispersed and somewhat isolated populations posing under different names; hence, the numerous synonyms. The populations which occur in the north central Pacific from Midway through Hawaii have been separately treated as *T. venusta* Deshayes (Dall, Bartsch, and Rehder, 1938). Individuals from this area are usually somewhat larger than typical *T. perna* from the central portion of the range and often possess reddish radiations on the beak. Such characters, for example, are relatively rare in populations from the Philippines, but in East Africa, individuals with reddish umbonal rays and slightly blunt posterior rostrations have been called *T. semilaevis* von Martens. Other variations that have been named include specimens with bright yellowish coloration, *T. sulphurea* Lamarck, those living in the Red Sea, *T. pharaonis* Hanley,

and those with slightly strengthened sculpture ventral to the posterior rostration, *T. tenuisulcata* Sowerby. None of these phenotypic variations is consistent enough to be of specific significance, and when large suites of specimens from all over the Indo-Pacific area are compared, it becomes evident that only a single species is involved.

Tellina vulsella, another species of *Pharaonella*, living in the Philippines and Japan, is thereby partially sympatric with *T. perna* and very closely related to it. Since the taxonomy of *T. vulsella* has been in confusion, I include its synonymy:

Tellina vulsella Hanley 1846 [*in*] Sowerby, Thes. Conch., 1: 235, pl. 61, figs. 162–163 (type-locality, Isle of Zebu [Philippine Islands]; type, BMNH no number).

Tellina sieboldii Deshayes 1854, Proc. Zool. Soc. London [1855 (May)], pt. 22, no. 282: 368 (type-locality, Japan; syntypes, BMNH no number).

Tellina perrieri Bertin 1878, Nouv. Arch. Mus., Paris, (2) 1: 255, pl. 8, fig. 8a-b (type-locality, Japan; syntypes, MNHNP).

Tellina consanguinea Sowerby 1903, Ann. Mag. Nat. Hist., (7) 12: 500 (type-locality, Hirado Hijan, Japan; holotype, BMNH 1903.12.7.1).

Since the *T. vulsella* of Chemnitz from the first edition of the Conchylien-Cabinet is not available, the first valid introduction of the name was by Hanley (1846). There is no doubt that this nomen is attached to the pharaonoid species of Japan and the Philippines. The species is typically reddish or flesh colored; it does not attain the size of *T. perna,* is more narrowly elongate, and has a more pronounced posterior rostration and greater compression.

The variety of colors found in *T. perna* is considerable. Although it appears that most specimens are white with some central suffusion of yellow, other individuals are completely permeated with lemon yellow. Reds and pinks are also frequently encountered, and occasionally the umbonal area may be rayed and suffused with pink. Bands of weak red occur much less frequently than bright rays, which extend from the umbo to the distal margins of the valves. The rays tend to be most broad and most intense posteriorly. More intensely banded and colored specimens are frequently found east of New Guinea.

The sculpture is also quite variable, as is the posterior outline of the shell. Younger individuals may possess fairly strong concentric lirations, which are usually more distinct in the right valve. Usually larger individuals are quite smooth, though some retain vestiges of stronger sculpture in the region of the posterior sulcus. Specimens with such sculpture, whose ventral margins are indented postbasally and are therefore more distinctly rostrate, have been called *T. tenuisulcata* or *T. pharaonis.* As noted previously, relatively large suites of specimens and good samples of the population show these characters to be inconstant.

Range. Tellina perna lives from Natal, South Africa, throughout the Indian Ocean, Indonesia, and the Philippines to Japan in the north, Australia in the south, the Samoan Islands in the southeast and the Hawaiian Islands in the northeast. It dwells in relatively shallow water in sandy substrates.

Specimens examined. REPUBLIC OF SOUTH AFRICA: Durban, Natal (BMNH; DM; NM; SAM; USNM). MOZAMBIQUE: Inhaca (ANSP; MCZ); Santa Carolina Id., Bazarutto Bay (MCZ). TANZANIA: Zanzibar (BMNH; MCZ); Bweju (USNM); Chumbe Id., in 0–6 ft., Mazizini, in mud and grass, Nguruwe Id., in 5–11 fms., and Ukombi Id., in 6–9 fms., all Zanzibar (all ANSP). EGYPT: Suez (BMNH). ADEN PROTECTORATE: Aden (BMNH). MADAGASCAR: (BMNH). Anakao, 20.5 mi. S of Tuléar (MCZ); Andilana and Nosy Antsaibory (ANSP); 1–2 mi. S of Nosy Iranja, white sand, in 11 fms. (ANSP).

SEYCHELLES IDS.: N.W. Bay, Mahe (BMNH). MAURITIUS: (BMNH). MALDIVE IDS.: S half of Kendikolu Id., 5°57′N; 73°24′E, Miladummadulu Atoll (ANSP); Kuda Huvadu, S Nilandu Atoll (ANSP). CEYLON: (MCZ). ANDAMAN IDS.: (BMNH). MALAYSIA: Singapore: (BMNH). THAILAND: Phuket Id. (ANSP). INDONESIA: Batavia, Java (MCZ; USNM); E Mios Woendi Id. and Konori Id., Padaido Ids. (both ANSP); E side Rouw Id., W side of Abroeki, 1 mi. SW of Maransabadi, Aoeri Ids., Geelvinck Bay (both ANSP). CHINA: Shanghai (MCZ). JAPAN: Sagami Bay (ANSP); Kyoto (MCZ); Wakayama (ANSP); Osima Osumi (? van Dieman Strait) (MCZ); Abu and Ishikawa Beach, Okinawa, Ryukyu Ids. (both USNM). PHILIPPINE IDS.: cove, S side of Corregidor Id., in 11 fms. (ANSP); east end of Sisiman Bay, Bataan, in 8 fms. (ANSP); Tilic Bay, Lubang Id. (MCZ); Jolo (USNM). AUSTRALIA: Abrolhos Ids. (USNM); Monte Bello Ids., Dampier Archipelago (BMNH); Port Essington, Northern Territory (BMNH); Moreton Bay, Queensland (MCZ). PALAU IDS.: Eil Malk, off Eomogan Id., 4 mi. SW of Eil Malk, in 3 ft., sand, west entrance of Kossol Passage, in 20 fms. and 1 mi. S of west passage Babelthuay Id. (all ANSP). MARSHALL IDS.: Bikini (USNM). SOLOMON IDS.: Ataa, Malaita Id. (ANSP). NEW CALEDONIA: (BMNH; MCZ); Bourail (ANSP); 2 1/2 mi. N Dumbea Pass, off Noumea, in 60 ft., sand (ANSP). FIJI IDS.: E end of Thakau Tanau Reef, 4–5 mi. NW of Port Ellington, NE Viti Levu; 1 1/2 mi. NE of Mbau Id., Viti Levu (both MCZ). SAMOA: Tutuila Id. (USNM). HAWAIIAN IDS.: Midway Id. (ANSP); Pearl and Hermes Reef (USNM); off Honolulu, in 6–8 fms., Oahu (ANSP; USNM); off Kaanapoli, in 4–8 fms., Maui (USNM).

Subgenus *Eurytellina* Fischer

Peronaeoderma 'Poli' Stoliczka 1870, Cretaceous Fauna of Southern India, vol. III: 116 (type-species, *Tellina punicea* Born 1778, original designation), *non* Poli 1795, *nec* Mörch 1853.

Eurytellina Fischer 1887, Manuel de Conchyliologie, p. 1147 (type-species, *Tellina punicea* Born 1778, monotypy).

Tellinota Iredale 1936, Rec. Aust. Mus., 19 (5): 281 (type-species, *Tellinota roseola* Iredale 1936, original designation).

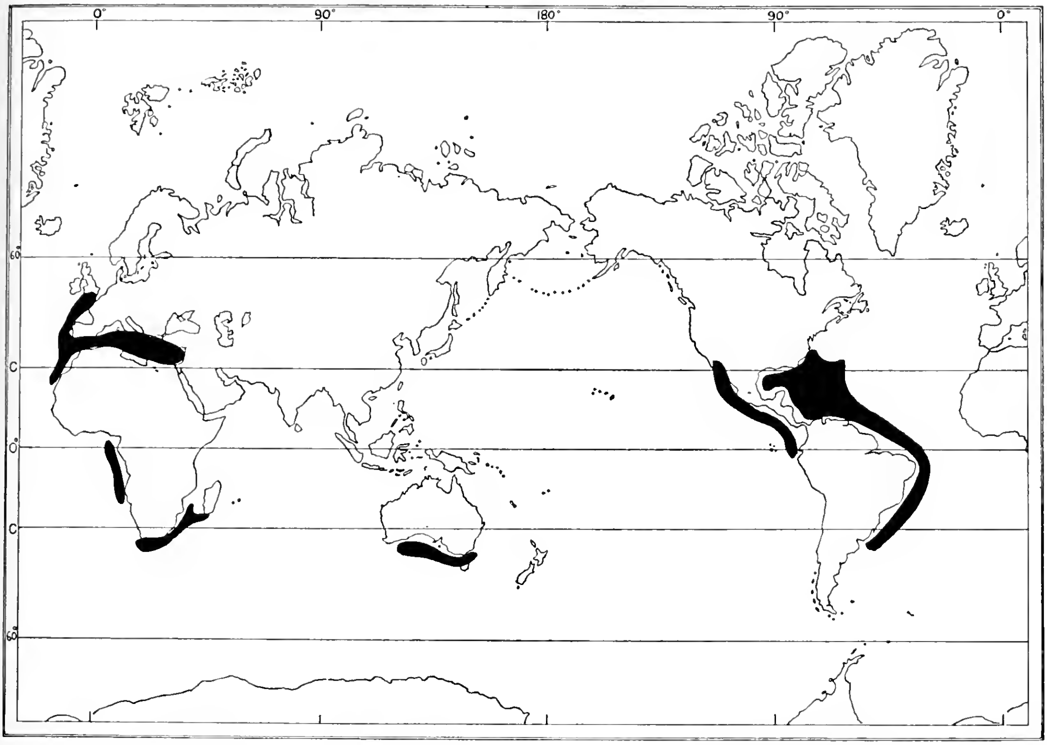
Description. Shell elongate-elliptical to subtrigonal, somewhat compressed and slightly inequilateral; posterior flexure to the right, weak, obsolete or absent; surface sculpture rather poorly developed; ligament posterior more or less protuberant, and strong; lateral teeth of the left valve poorly developed, with a weak, tubercle-like proximal anterior tooth and an obsolete distal posterior lateral tooth; in the right valve, the distal posterior is often well developed and the proximal anterior is generally well developed and strong; pallial sinus rather flattened dorsally and extending far anteriorly, near to or contiguous with the anterior adductor; confluence of the pallial sinus with the pallial line extensive.

The group of *Eurytellina* forms a natural assemblage of species characterized by the right lateral dentition, the more or less elongate elliptical shape of the shell, the compression of the valves, and the relatively smooth superficial sculpture on the anterior slope and disc of each valve. Many of the species are highly or intensely colored with reds, pinks, and apricots.

Although *Eurytellina* appears to be most highly evolved in the western Atlantic-eastern Pacific region, it is represented in the eastern Atlantic and Mediterranean by *T. incarnata*, in tropical west Africa by *T. madagascariensis*, in cool temperate South Africa by *T. alfredensis* and in the Australian region by *T. albinella* and *T. roseola*. Map 4 shows the distribution of *Eurytellina*.

Tellina (Eurytellina) alfredensis Bartsch
Plate 9, figures 1, 2; Plate 10, figure 2.

Tellina rosea Spengler 1798, Skrivter af naturhistorie Selskabet København, 4 (2): 83 (type-locality, Fra Niquebar, here corrected and



Map 4. The distribution of species of *Eurytellina*. The species include: in South Africa, *alfredensis* and *prismatica*; in West Africa, *madagascariensis*; in Australia, *albinella* and *roseola*; in the northeastern Atlantic Ocean and Mediterranean Sea, *incarnata*; in the western Atlantic, *punicea* and allies (*alternata*, *tayloriana*, *angulosa*, *nitens*, *trinitatis*, *guildingii*, *vespuciana*, and *lineata*); and, in the eastern Pacific, *simulans* and allies (*laceridens*, *hertleini*, *laplata*, *eburnea*, *rubescens*, *ecuadoriana*, *inaequistriata*, *mantaensis*, and *prora*). The group is obviously most highly differentiated in the New World, where it is predominantly tropical. In the Indo-Pacific and European areas it tends to occupy cooler waters.

restricted to Port Alfred, South Africa; types, ? Zoological Museum, Copenhagen; refers to Chemnitz 1782, Conch.-Cab., vol. 6: 105, fig. 96), *non* Gmelin 1791 *nec* Crouch 1827.

Tellina albinella alfredensis Bartsch 1915, Bull. U. S. Nat. Mus., 91: 205, pl. 46, figs. 7, 8 (type-locality, Port Alfred, South Africa; holotype, USNM 186948).

Tellina madagascariensis 'Gmelin' Barnard 1964, Ann. South African Mus., 47: 537, fig. 41a, *non* Gmelin 1791.

Description. Shell extending to 85 mm in length and to 53 mm in height, elongate-sublanceolate, nearly equilateral, solid, more or less compressed, with left valve of greater convexity than right, and with definite flexure to right posteriorly. Umbo central (little anterior in younger specimens), little elevated or inflated, white and blunt; umbonal cavity shallow and rather filled in, particularly in right valve. Anterior margin convex, narrowly and smoothly rounded; ventral margin long, gently convex, rising in arcuation posteriorly, some specimens with postbasal concave indentation; anterior dorsal margin long, gently sloping, and weakly convex to straight; posterior dorsal margin long, slightly more steeply descending, straight to slightly concave; posterior short, generally quite distinct, straight to weakly convex. Sculpture consisting of extremely weak and very closely spaced concentric threads and of extremely fine radial vermiculations; concentric lamellations present

on posterior third of discs and posterior dorsal slope of right valve (about 2 per mm). Growth lines evident, particularly in large individuals, and often coincident with concentric bands of darker or lighter coloration. Two posterior radial ridges with sulcus between in each valve, though stronger in right valve; distal biangulation of ridges nearly define extent of posterior margin; single anterior radial ridges define anterior dorsal margin, sharper in right valve.

Ligament brownish, strong, not protuberant, set into elongate, lanceolate escutcheon defined by dorsalmost radial ridges; calcareous portion of ligament elongate and subtended by narrow nymphal callosity. Elongate, thin, external horny ligament anteriorly. Hinge line moderately well developed. In left valve, cardinal complex consisting of anterior, subdeltoid, bifid cardinal tooth with subequal lobes, and of posterior, thin, laminate cardinal tooth generally obsolete, missing, or coalescent with anterior border of calcareous portion of ligament; anterior lateral tooth obsolete, consisting of subproximal thickening of hinge line; posterior lateral tooth obsolete or missing, consisting of weak distal enlargement of hinge line. In right valve, cardinal complex consisting of rather thin anterior cardinal tooth and of subdeltoid, bifid, posterior cardinal tooth with subequal lobes; anterior lateral tooth subproximal to cardinal complex, moderately strong, and little upcurled; posterior lateral tooth distal, grooved above, slightly protuberant, and weaker than anterior lateral tooth.

Muscle scars well impressed. Anterior adductor scar irregularly rounded, semilunate; posterior scar rounded, subquadrate. Pallial sinus hardly rising, gently arcuated and falling to pallial line in anterior quarter of its length, and widely separated from anterior adductor muscle scar. Cruciform muscle scars closely adjacent to pallial line, irregularly subequal. Color predominantly pink, pinkish red, and white; rarely with apricot-orange hues. Internally, red coloration stronger and more definitive. Externally, white and reddish often disposed in bands of no apparent pattern or regularity; hinge line and dorsal margins white internally.

Length mm	Height mm	Width mm	
84.4	52.9	—	Hermanus Beach [right valve only]
78.6	43.2	—	Still Bay
72.3	43.1	15.9	Still Bay
70.8	41.6	16.4	Algoa Bay
46.5	26.0	08.8	holotype of *alfredensis*
40.9	22.0	07.0	Knysna
38.2	20.5	06.4	Jeffreys Bay
28.8	14.7	—	Knysna (right valve)
20.5	11.1	—	Knysna (left valve)

Remarks. Tellina rosea Spengler is preoccupied by *T. rosea* Gmelin and Bartsch's name, *T. alfredensis,* the next available synonym, has to be used. It is necessary, however, to remark on the historical usages of the name *rosea* Spengler, as well as on the species *madagascariensis* Gmelin, which has often been confounded with the former. There has been considerable confusion in the appropriate name by which *T. alfredensis* should be known. The question is an historical one, and reference to the early literature is necessary. Furthermore, the assignations of type-localities for the species have been difficult. As indicated in the synonymy, *Tellina rosea* Spengler is based on a figure of Chemnitz (1782, vol. 6: 105, fig. 96). *Tellina madagascariensis* Gmelin is based on a figure of Lister (1770, pl. 386, fig. 233). The illustrations are herein considered as type-figures for the respective names. The type-localities of both *rosea* Spengler and *madagascariensis* Gmelin were originally in error. Chemnitz (1782) expressed doubt as to the exact geographical occurrence of *rosea* Spengler when he remarked: "Sie wohnet vermuthlich in den ostindischen Gewässern. Doch bekenne ichs gerne, dass mir ihr wahres eigentliches Vaterland mit keiner Gewissheit bekannt worden sey." Chemnitz's specimen came from Spengler's collection and is presumably in the Zoo-

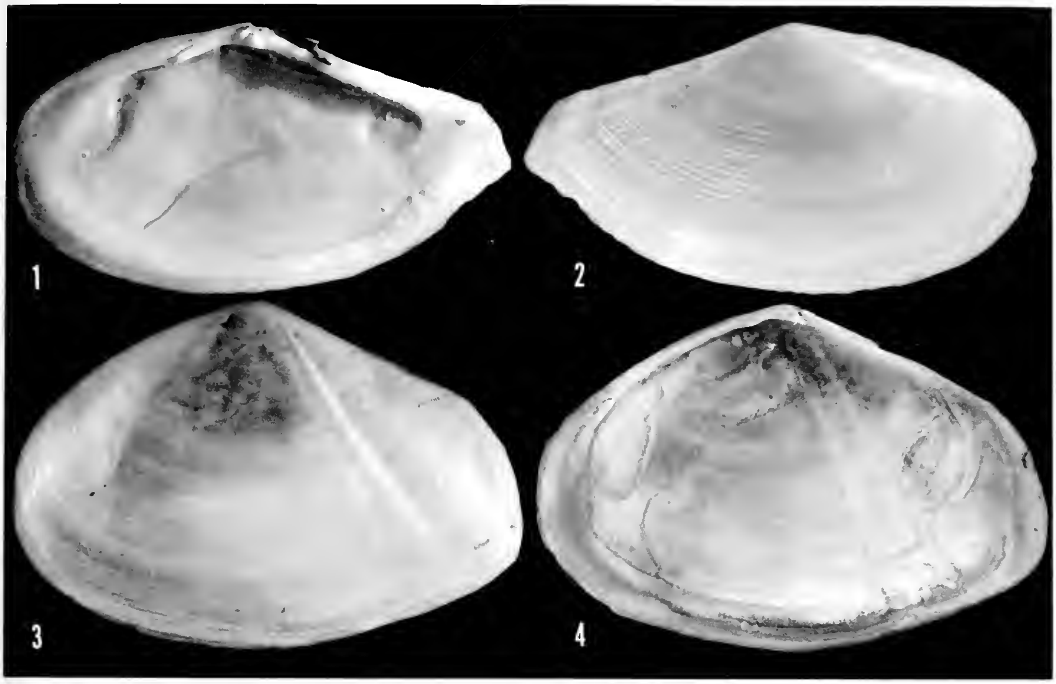


Plate 9. Figs. 1 and 2. *Tellina (Eurytellina) alfredensis* Bartsch, Still Bay, South Africa, SAM A30018 (length = 41 mm): Fig. 1, internal view of the right valve; Fig. 2, external view of the right valve. Figs. 3 and 4. *Tellina (Tellinides) opalina* Gmelin, Chinde, Mozambique, SAM A6181 (length = 26 mm): Fig. 3, external view of the left valve; Fig. 4, internal view of the right valve.

logical Museum in Copenhagen. Yet Spengler (1798) was able to give a locality for *T. rosea* as 'Fra Niquebar,' which refers to the Nicobar Islands in the Bay of Bengal. Gmelin (1791) gives Madagascar as the type-locality for *T. madagascariensis* and this error was derived from Lister, whose figures indicate the locality.

The range of *T. madagascariensis* has been given by Nicklès (1950) as from the French Congo to Angola. Reference to the literature and museum specimens substantiates his statements and adds more specific data. From north to south, the documented range of *madagascariensis* is: São Thome (Nobre, 1909); Cape Lopez (USNM 348320); Mayumba, Gabon (Nicklès, 1952); Loango, Brazzaville, Congo (Nicklès, 1952); Loanda, Angola (Hoyle, 1887); Lobito and Moçâmedes, Angola (Dautzenberg, 1912; Paes da Franca, 1960b); Great Fish Bay (Dautzenberg, 1912; Thiele and Jaeckel, 1931) [= Baia dos Tigres] and Cape Negro, Angola (Odhner, 1923). The locality Porto Grande, St. Vincent, Cape Verde Islands, given by Stearns (1893), is based upon 2 dead and beach worn shells (USNM 125365) and therefore cannot be construed as evidence that the species lives there. Thus, more specifically, *T. madagascariensis* ranges from off São Thome and Cape Lopez, Gabon, south along the west coast of Africa to the Baia dos Tigres in the Porto Alexandre Park of Angola just north of Kunene River. The localities Rio de Janeiro and Sénégal given by Bertin (1878) are clearly in error. A single right valve of *T. madagascariensis*, probably ballast, was collected by de Villiers at Jeffreys Bay, Humansdorf Coast, Cape Colony (USNM 382492), and a single left valve has been

found in deposits at the mouth of the Klein River (SAM A 30017).

Tellina alfredensis appears to be exclusively South African while *T. madagascariensis* occurs along the coast of West Africa and does *not* occur in Madagascar. The type-locality of *T. rosea* Spengler [= *alfredensis*] is here corrected and restricted to Port Alfred, in agreement with the type-locality of *alfredensis,* and the type-locality of *T. madagascariensis* is here corrected and restricted to Loanda, Angola, West Africa.

The assumption of Salisbury (1934) that *Tellina dautzenbergi* Nobre 1894 was a synonym of *Tellina rosea* Spengler, *non* Gmelin, is incorrect. Nobre's figure, though not particularly good, is identical with *Tellina mars* Hanley of West Africa. Among other things which indicate that *dautzenbergi* is not *rosea* Spengler [= *alfredensis*] is the fact that *dautzenbergi,* which is from São Thome, is outside the range of *alfredensis.*

There have been two species with which *T. alfredensis* has been confused, namely, *T. madagascariensis,* a close relative, and *T. albinella,* an even more closely related species. A comparison and discussion of these two species follow.

The most singularly distinguishing characteristic that serves to contrast *T. alfredensis* and *madagascariensis* is the configuration of the pallial sinus (see Pl. 10, figs. 2–3). In *alfredensis,* the pallial sinus is widely separated from the anterior adductor muscle scar whereas in *madagascariensis,* it is confluent or nearly confluent with the anterior adductor scar. Further, the anterior adductor muscle scar of *madagascariensis* is much longer and larger than that of *alfredensis.* The species may even be distinguished externally. In *alfredensis,* the posterior outline differs from that of *madagascariensis* in being concavely arcuate ventrally and more definitively pointed posteriorly. The posterior ridge in *alfredensis* is more sharply defined and more closely parallel to the posterior dorsal margin than in *madagascariensis.*

Tellina alfredensis has often been confused with *T. albinella* Lamarck of South Australia, and, indeed, was described as a subspecies of *albinella.* For all of Bartsch's ability to distinguish species on even the most flimsy of grounds, it is remarkable that he never considered *alfredensis* as a distinct species. Van Bruggen (1952) compared *alfredensis,* which he called *rosea,* with *albinella* and concluded that they differed in heaviness. The similarity in the structure of the dentition of the right valve and in the general configuration of the pallial sinus indicates the close relationship. Further, they are very similar in shape and are both highly colored. However, they differ in so many features that there is no question that they are separate species (Pl. 10, figs. 1–2). *T. albinella* has a shell that is much thinner and therefore not as heavy as that of *alfredensis.* In conjunction, the right anterior lateral tooth is more proximal to the cardinal complex, and the cardinal teeth are consequently strengthened, with the right posterior bifid cardinal tooth considerably enlarged and protuberant. In *albinella,* the pallial sinus curves posteriorly as it coalesces with the pallial line, whereas in *alfredensis,* the pallial sinus maintains its gentle convexity and unites with the pallial line without such a curvature. The posterior margin is not as distinctly defined in *albinella* as it is in *alfredensis,* and there is only a slight, if any, flexure to the right posteriorly in *albinella,* whereas in *alfredensis* the posterior flexure is rather strong. As stated previously, both species have highly colored shells, but *alfredensis* is predominantly of a pink or reddish suffusion whereas *albinella,* though having pinks and reds, has a tendency to be suffused with apricot internally and may even be nearly pure white.

The unique structure of the anterior dorsal margin of *alfredensis* is elaborated by what I have called the anterior ridges.

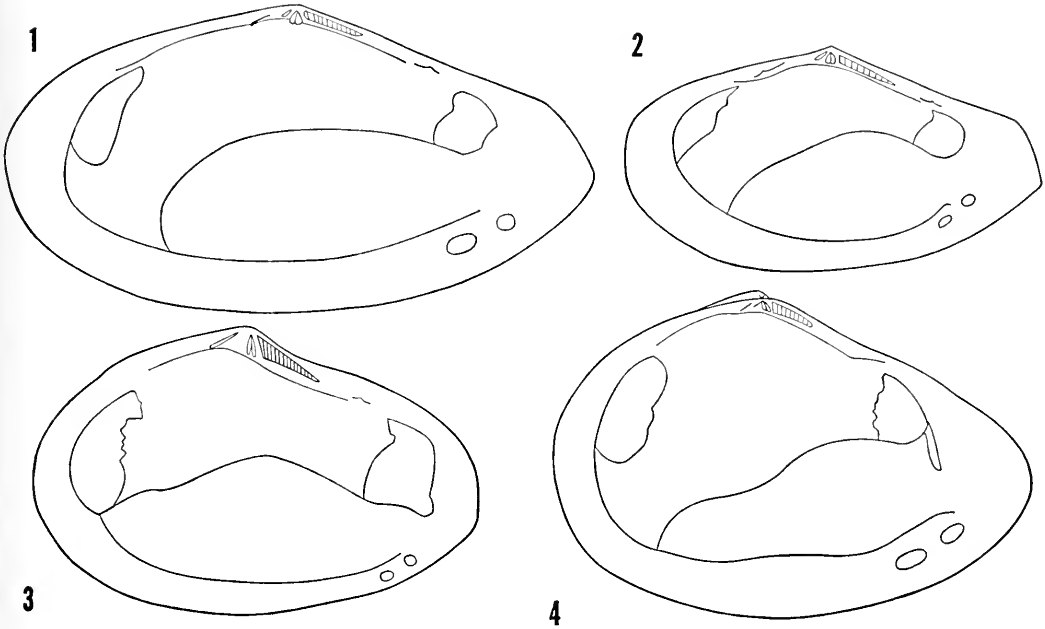


Plate 10. Diagrammatic illustrations of the internal surface of the valves, showing the dental configuration and muscle scars. Fig. 1. *Tellina (Eurytellina) albinella* Lamarck: right valve, South Australia, USNM 321610 (length = 32 mm). Fig. 2. *Tellina (Eurytellina) alfredensis* Bartsch: Right valve, Still Bay, South Africa, SAM A30018 (length = 21.2 mm). Fig. 3. *Tellina (Eurytellina) madagascariensis* Gmelin: right valve, Porto Grande, St. Vincent, Cape Verde Islands, USNM 125365 (length = 75 mm). Fig. 4. *Tellina (Homalina) trilatera* Gmelin: right valve, Muizenberg, False Bay, South Africa, USNM 617728 (length = 26.7 mm).

In the right valve the ridge is much stronger, more sharply formed, and higher than in the left valve. Therefore, when the valves are adpressed, the right valve is slightly higher than the left and there is a deep cleft like an elongate lunule between the valves in the median longitudinal axis. The sheer entad walls formed by these ridges, particularly in the right valve, create a broad margination when the internal surface of the valve is viewed. At the bottom of this cleft, toward the umbos, an anterior external horny ligament is developed. Such a structure is not unusual in the Tellinidae, and Owen (1958) has pointed out these various parts of the ligament in detail. Only the conspicuous posterior ligament, with its well-developed external and internal portions, has generally been included in descriptions—usually because this anterior ligament is obscure and very often lost. But in *T. alfredensis* it is much more strongly developed and even conspicuous in adults. Occurrences of this species in the fossil record are numerous; they have been fully listed and documented by Barnard (1962b; 1964b).

Range. In South Africa, this species lives from the Cape of Good Hope to Port Alfred. Since it has been found in the Pleistocene north of Swakopmund, it may occur alive off the coast of South West Africa, but I have seen no specimens from that area. Records from West Africa, i.e. the Congo or Angola, are for true *T. madagascariensis*. *T. alfredensis* seems to prefer off-shore cool water habitats in sand and shell substrates and has been taken alive to 37 m. Although I have not seen specimens from Madagascar, a number of reports signal its occurrence on that island (see Dautzenberg, 1929).

Specimens examined. REPUBLIC OF SOUTH AFRICA: (BMNH); Cape of Good Hope (MCZ); Muizenberg, False Bay (UCT; USNM); Hermanus Beach, Caledon Coast (USNM); Riversdale District, Still Bay (SAM; MCZ); N of Cape Seal, Plettenberg Bay (UCT); Knysna (SAM); Jeffreys Bay (DM; MCZ; USNM); Green Island, Port Elizabeth (DM); Algoa Bay (ANSP; MCZ; NM); Port Alfred (BMNH; MCZ); near Grahamstown, Port Alfred (USNM).

Tellina (Eurytellina) prismatica Sowerby
Plate 11, figure 1; Plate 12, figures 1, 2.

Tellina prismatica Sowerby 1897, Appendix to Marine Shells of South Africa, p. 22, pl. 6, fig. 29 (type-locality, Durban; syntypes, BMNH 99.4.14-.2952 and 1905.10.23.55), *non* Sowerby 1905.

Description. Shell extending to 20 mm in length and 12 mm in height; sublanceolate to subtrigonal; inequilateral, equivalve, fragile to solid, rather compressed, with left valve of slightly greater convexity and with slight flexure to right posteriorly. Umbo slightly behind middle, slightly elevated, pointed, and inconspicuous; umbonal cavity shallow. Anterior margin smoothly and narrowly rounded; ventral margin more or less straight, rising slightly posteriorly; anterior dorsal margin elongate, straight to slightly convex, and gently descending; posterior dorsal margin relatively short, steeply descending, and irregularly convex; posterior margin short, forming blunt posterior, oblique truncation. Sculpture consisting of more or less regular, finely incised sulcations (about 8 to 12 per mm); no true radial sculpture, but radial vermiculations sometimes present. Posterior ridge in right valve variously developed, and concomitant sulcus present in left valve. Concentric growth lines often conspicuous.

Ligament short, protuberant, yellowish brown, set in weakly defined short sublanceolate escutcheon; no true lunule developed. Calcareous portion of ligament moderately developed and subtended by slightly raised nymphal callosities. Hinge line rather strongly developed. In left valve, cardinal complex consisting of anterior narrow, bifid tooth with subequal lobes, and of posterior elongate, thin laminate cardinal tooth; anterior lateral tooth subproximal to cardinal complex, consisting of slightly thickened to strongly thickened denticle on hinge margin; posterior lateral tooth at distal end of ligament, slightly socketed above, consisting of protuberant, slightly pointed thickening. In right valve, cardinal complex consisting of posterior, skewed, subdeltoid bifid tooth with subequal lobes, and of anterior strong, protuberant cardinal tooth; anterior lateral tooth subproximal to cardinal complex, strong, usually thickened and protuberant, sometimes narrow and upcurled; posterior lateral tooth distal, at posterior end of hinge line, narrow, shelf-like, slightly upcurled, and socketed above. No true rib developed.

Muscle scars moderately to well impressed. Anterior adductor muscle scar irregularly sublunate and posterior adductor muscle scar irregularly subquadrate. Pallial sinus equal in both valves, rising sharply behind, gently arcuate dorsally, falling in more or less straight line to base of anterior adductor muscle scar; confluence entire. Cruciform muscle scars generally well impressed, small, rounded, except right anterior rectangular scar. Shell white, suffused with red, pink, or rarely flesh colored, sometimes arranged in bands. Umbos generally white.

Length mm	Height mm	Width mm	
19.4	10.5	05.4	Durban Bay
18.0	11.7	06.2	Richards Bay
15.0	09.5	04.5	Durban Bay
12.0	06.6	02.6	Durban Bay
11.4	06.9	03.1	Durban Bay
08.2	04.5	—	Off Tegula River
07.8	04.6	—	Off Tegula River

Remarks. Sowerby (1897) described *T. prismatica* from Durban and mentioned that it was very thin, compressed, elongate, and iridescent. However, the definitive

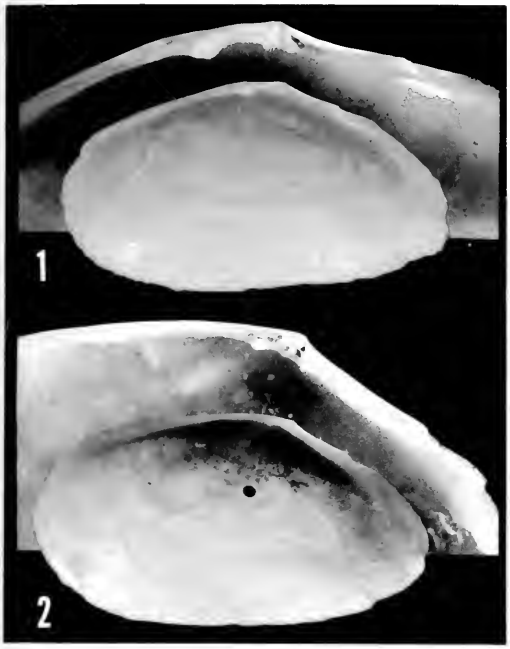


Plate 11. Fig. 1. *Tellina* (*Eurytellina*) *prismatica* Sowerby: internal view of the right valve and enlargement to show placement of the right anterior lateral tooth, Durban Harbor, NM (length = 19.4 mm). Fig. 2. *Tellina* (*Tellinides*) *natalensis* Philippi: internal view of the right valve and enlargement to show the right anterior lateral tooth nearly coextensive with the cardinal complex, Durban Harbor, NM (length = 21.3 mm).

diagnostic traits that serve to identify *T. prismatica* are not those related to the thinness of the valves, but include the strong dentition in the right valve, with the anterior lateral tooth rather proximal to the cardinal complex, and the configuration of the pallial sinus, which touches or nearly extends to the anterior adductor muscle scar. Also, the development of the left lateral dentition is another important diagnostic character which distinguishes this species.

Again we are confronted with a small tellen that exhibits a considerable range of variation. As indicated in the description, the valves may be fragile to solid. Smaller individuals usually tend to be transparent and thin-shelled, whereas individuals that approach the maximum size tend to be more heavily shelled. The shape is also variable, but most often elongate-sublanceolate specimens are encountered; strongly shelled, subtrigonal or subquadrate specimens do occur, however, and very much resemble *T. yemenensis* in structure, except that they lack the posterior rostration and apricot coloration of that species.

As Sowerby remarked, *T. prismatica* resembles *T. valtonis* from the Red Sea. Indeed, there are a number of species that have never been really completely described, which I have not had available, that belong to the complex of smaller tellens. In addition to *valtonis*, mention should also be made of *T. flacca* Römer, *T. hilaris* Hanley, *T. arsinoensis* Issel, *T. scitula* H. Adams, *T. erythraea* Römer, *T. nitens* Deshayes, and *T. felix* Hanley. *T. prismatica* might well be synonymous with one of them. Specimens that Barnard (1964b) discussed as *T. natalensis* and that Day and Morgans (1956) referred to as *T. scalpellum* are really *T. prismatica.*

Range. *T. prismatica* lives in the warmer waters of the Natal coast of South Africa.

Specimens examined. REPUBLIC OF SOUTH AFRICA: Durban Bay (BMNH; NM). Richards Bay estuary, Zululand (UCT-ES); all near mouth of Tegula River, 29°10′S, 31°51′E in 43 meters, 29°21.6′S, 31°35.7′E in 57 meters, coarse mud, sand, and shell, and 29°19.8′S, 31°26.2′E in 38 meters, coarse sand (all UCT-ES).

Subgenus *Tellinides* Lamarck

Tellinides Lamarck 1818, Anim. sans Vert., 5: 535 (type-species, *Tellina timorensis* Lamarck 1818, original designation).

Description. Shell of small to medium size (to 60 mm), elongate-subrectangular, rarely transversely subtrigonal, inequilateral, rather compressed, and slightly gaping posteriorly. Umbos rather small, inconspicuous, and usually median to anterior in position. Ligament moderately strong, protuberant. Dentition weak; cardinal teeth normal; lateral teeth obsolete or absent except for right anterior peglike

tooth, closely juxtaposed to cardinal complex. Pallial sinus rising sharply behind, pointed in apex dorsally beneath umbo, descending in oblique line anteriorly, and uniting with pallial line some distance from anterior adductor muscle scar. Tracts of cruciform muscle scar often marked by whitish ray posteriorly. Color purple-red to white.

Remarks. Certainly the lineage of *Tellinides* is close to that of *Homalina*, since large individuals of *T. opalina* are extremely similar to *T. trilatera.* The closely proximal right anterior lateral tooth also indicates the propinquity of *Tellinides* and *Homalina.* I use *Tellinides* separately, because its aforementioned dental element is generally strong and peglike, its shell very often highly colored, with posterior rays that indicate the attachment tracts for the cruciform muscles, and the outline of its valves, though at times subtrigonal, tends to be elongate-sublanceolate or subrectangular.

It should also be mentioned that *Tellinidella* Hertlein and Strong, represented by the eastern Pacific *Tellinides purpureus* Broderip and Sowerby 1829, must be a distant offshoot of the *Tellinides* lineage. That species is extremely highly colored with purple-red but has a single slight subproximal right anterior lateral tooth. Both characters are very reminiscent of what is found in species such as *T. opalina* or *T. timorensis*, and, for that matter, in *T. lanceolata* Linnaeus, the type-species of the controversial *Angulus.*

Tellina (Tellinides) opalina Gmelin
Plate 4, figures 3, 4; Plate 9, figures 3, 4.

Tellina apelina (*sic*) Gmelin 1791, Syst. Nat., ed. 13, p. 3236 (type-locality, in sinu Nicobarico; types, possibly in Spengler collection, Copenhagen; refers to Chemnitz, 1782, Conch.-Cab., vol. 6: 118, pl. 12, figs. 107 [108]).[1]

Tellina opalina Gmelin. Spengler 1798, Skrivter af naturhistorie Selskabet København, 4 (2): 106; Bosc 1801, Hist. Nat. Coq., 3: 26; Link 1807, Beschr. Nat. Samml. Univ. Rostock, 3: 147, *non* Sowerby 1868.

Tellinides rosea Crouch 1827, Lamarck's Conch., pp. 11 and 44, pl. 4, figs. 1a and b (type-locality not given, supposed to be from the Indian Ocean; types, not known); Sowerby 1828, Genera of Recent and Fossil Shells, pt. 31, *non* Gmelin 1791, *nec* Spengler 1798.

Tellina planissima Anton 1839, Verzeichniss, p. 4 (type-locality not given; types, not known); 1844 [*in*] Philippi, Abbild. Beschreib. Conch., vol. 1, *Tellina*, p. 123 [11], pl. 2, fig. 2 (type-locality, insulae Moluccae . . .).

Tellina (Angulus) immaculata 'Philippi' Barnard 1964, Ann. S. Afr. Mus., 47: 544, *non* Philippi 1849.

Description. Shell extending to 49 mm in length and to 33 mm in height, subrectangular to subacuminate, slightly inequilateral, nearly equivalve, usually rather thin and translucent in younger individuals, large adults sometimes subsolid, compressed, with right valve slightly more convex and with slight flexure to right posteriorly. Umbos subcentral, slightly in front of middle, white or pink and pointed. Anterior margin broadly and smoothly rounded; ventral margin broadly convex, rising in gentle convex arcuation posteriorly; anterior dorsal margin gently descending and slightly convex; posterior dorsal margin more sharply descending, long and more or less straight; posterior margin slightly convex, forming somewhat oblique truncation. Sculpture consisting of finely incised, closely spaced (4–7 per mm) concentric sulcations, frequently somewhat scissulate along anterior slope and stronger along posterior dorsal slope; radial vermiculations most evident on central disc. Posterior ridge weakly developed and poorly defined.

Ligament reddish brown to black, moderately strong, and protuberant. No true lunule present. Calcareous portion of ligament set upon slightly elevated nymphal callosities. Hinge rather weakly developed. In left valve, cardinal complex consisting of anterior, narrowly compressed, bifid tooth with subequal lobes and of posterior

[1] Chemnitz listed this species, ex museo Spengleriano, a collection which is housed in Copenhagen Museum; he gave the locality as: "Sie wohnet an den nicobarischen Meerufern."

elongate single laminate tooth; no true lateral dentition; narrow, subproximal fold representing anterior lateral tooth. In right valve, cardinal complex consisting of posterior fragile bifid tooth, with posterior lobe larger and skewed posteriorly, and of anterior short, slightly thickened, but weak laminate tooth; anterior lateral tooth closely juxtaposed to cardinal complex, short, protuberant, peglike, sometimes slightly upcurled; no true posterior lateral tooth.

Muscle scars moderately well impressed. Anterior adductor muscle scar narrowed and subsemilunate; posterior muscle scar subrectangular, rounded posteroventrally, and with dorsal extension of posterior pedal retractor muscle scar. Pallial sinus more or less equal in opposite valves, rising sharply from posterior adductor muscle scar, irregularly descending in arcuation anteriorly, not coalesced with and separated from anterior adductor muscle scar, and joining pallial line ventrally in convex arcuation; confluence extensive. Distance separating anteriormost extension of pallial sinus and anterior adductor muscle scar variable. Posterior termination of pallial line hook-shaped. Cruciform muscle scars generally well impressed, large and rounded, more widely separated in right valve; internal thickened rib in left valve with very weak radial vermiculation before it and two more or less equal riblets in right valve, corresponding to attachment of cruciform muscles. Shells white peripherally with pinkish-red suffusions throughout; white rays conspicuous posteriorly, especially in left valve, corresponding to ribs supporting cruciform musculature.

Length mm	Height mm	Width mm	
48.8	32.2	08.2	Dapitan, Mindanao, Philippines
47.2	32.2	08.2	Lampinegan Id., Philippines
38.3	25.1	05.7	Durban
35.1	23.5	05.2	Durban
31.0	22.1	05.3	Lunga, Guadalcanal, Solomon Ids.
26.2	18.4	04.6	Chinde
21.8	13.9	03.6	Delagoa Bay

Remarks. Tellina opalina was first described by Chemnitz (1782). Schröter (1786; 1788) also referred to the species. Since these works are non-binomial, their names are not available for nomenclatorial purposes. Gmelin (1791) used *T. apelina,* an obvious misspelling or *lapsus;* subsequent authors have used the spelling *opalina.* Spengler (1798), Bosc (1801), and Link (1807) cited *opalina;* these references are not to be construed as homonyms, although they are entered individually in the Index Animalium. Salis-Marschlins' (1793) mention of this species is based on a misidentification; the species does not occur in the Mediterranean. As pointed out by Smith (1878), Sowerby (1868) described and figured an homonymous *T. opalina* which is not to be confused with *T. opalina* Gmelin.

Since Sowerby did not include authors' names in his plate captions for the *Genera,* the name *Tellinides rosea* has been attributed to Sowerby by Smith (1878). According to notes compiled by Dall in the U. S. National Museum, the plate on *Tellinides* was included in part 31 of Sowerby's *Genera;* Sherborn (1894) has shown that the date of publication of this part was 22 December 1828. Since Crouch's work (1827) antedates this, it appears that Sowerby was referring to Crouch's species. The name *Tellinides rosea* Crouch should not be confused with *Tellina rosea* Gmelin or *Tellina rosea* Spengler (see the synonymy of *T. alfredensis* Bartsch).

Barnard (1964b) called this species *T. immaculata,* which was described by Philippi (1849: 55, *Tellina* (p. 27), pl. 5, fig. 2) from Mergui in Burma and is an elongate species of low proportions with the pallial sinus confluent for a short distance posteriorly; the shell is white; it is very closely related to, and possibly synonymous with, *T. vestalis* Hanley; it is not closely related to *T. opalina* Gmelin.

There is no doubt that the East African populations of *T. opalina* differ from those inhabiting the Indonesian and Philippine

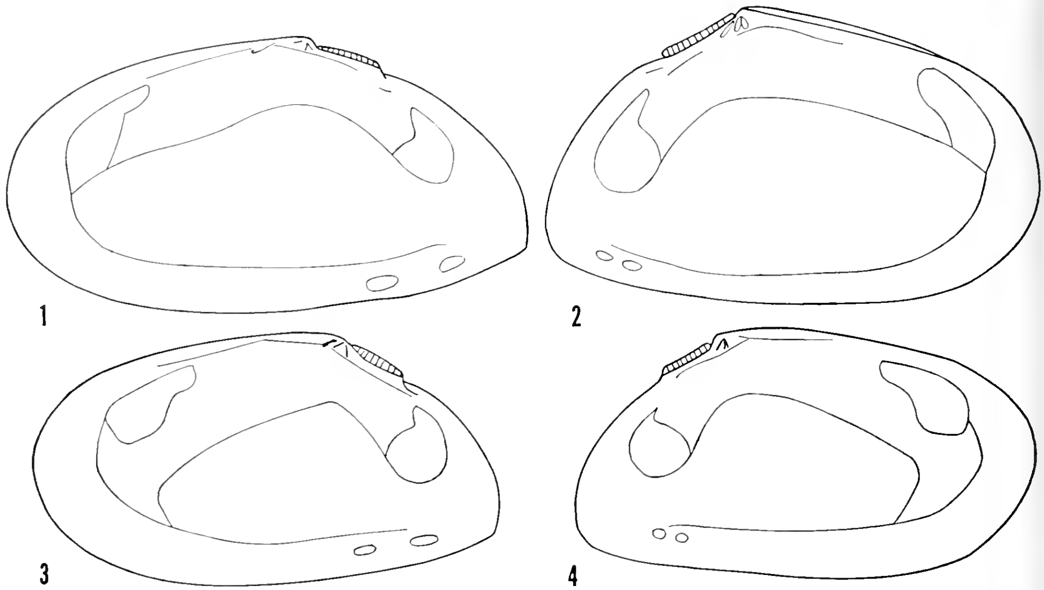


Plate 12. Diagrammatic illustrations of the internal surface of the valves showing the dental configuration and muscle scars. Figs. 1 and 2. *Tellina (Eurytellina) prismatica* Sowerby, Durban Harbor, NM (length = 19.4 mm): Fig. 1, right valve; Fig. 2, left valve. Figs. 3 and 4. *Tellina (Tellinides) natalensis* Philippi, Durban, DM (length = 17.2 mm): Fig. 3, right valve; Fig. 4, left valve.

regions. For example, the posterior margin of the Mozambique specimens is more oblique and less pointed. Smith (1878) also noted that the East African specimens were "more equilateral in form." None of the material I have examined from South or East Africa is as large as the specimens from the Philippines. However, in my opinion, these variations are not sufficiently great to be of specific significance. There is some indication that with increased size, the outline of the valves becomes increasingly more acuminate. Further, the placement of the pallial sinus alters with increased size. In smaller specimens the pallial sinus approaches the anterior adductor muscle scar more closely.

Large, whitish specimens of *T. opalina* may be very similar to large specimens of *T. trilatera*. The acentric sculpture on the postbasal surface of the right valve of *trilatera*, as well as the fact that the right anterior lateral tooth is almost incorporated into the cardinal complex of *trilatera*, serve to distinguish the species. Further, in *opalina* of this size (43 mm), the internal rib is well developed, and the umbo is not so far anterior.

Tellina adenensis Smith 1891 has been referred to *Tellinides* by Lamy (1918). This species is very similar to the *T. opalina* populations from East Africa, and I am tempted to place *T. adenensis* in the synonymy of *T. opalina*. Unfortunately, no specimens from the region around Aden were available for study.

Tellina sinuata Spengler 1798 [= *T. timorensis* Lamarck 1818] (see Hidalgo, 1903) is another relative of *T. opalina;* it is distinguished by its somewhat subquadrate outline and its different, less angulate, posterior slope.

T. opalina is conspicuous in its development of posterior radial ribs. The posteriormost rib of the left valve is the strongest and is thickened and white in color, so that it contrasts noticeably with the usual pinkish red of the shell matrix. The an-

teriormost rib of the left valve and the two slightly more divergent riblets of the right valve are all weaker, though they may be colored white and form conspicuous posterior rays. Functionally, these ribs or riblets are places of attachment and support for the cruciform muscles. It follows that the left posterior head of this muscle is the strongest of all four parts of the cruciform muscle.

Range. Tellina opalina is an Indo-Pacific species with two general areas of distribution. One group of populations is found in the western Indian Ocean as far south as Durban on the east African coast, while the main concentration of populations is in the East Indies, the Philippine Islands, and west to Fiji.

Selected literature references document the occurrences of the species: South Africa (Barnard, 1964b); Mozambique (mouth of the Macusi River, near Quelimane) (Smith, 1878); Tuléar, Ankilibé, and Tamatave, Madagascar (Dautzenberg, 1929); Persian Gulf (Melvill and Standen, 1907); Nicobar Islands (Chemnitz, 1782; Spengler, 1798); Lho Seumawe, Sumatra and Karange Hawae (Karang Hawo), Java (Adam and Leloup, 1939); Dapitan and Davao, Mindanao, the Philippine Islands (Hidalgo, 1903); the Moluccas (Philippi, 1849; Römer, 1871; Bertin, 1878).

Specimens examined. REPUBLIC OF SOUTH AFRICA: Durban Bay (DM; NM). MOZAMBIQUE: (BMNH) Delagoa Bay (SAM); mouth of the Zambesi River, near Chinde (SAM). INDONESIA: Tjiperwagaran, Keledjitan, and Pruput, Bantam, Java; Pelaboehan Ratoe, Java; Tanjong Aru, near Jesselton, North Borneo (all USNM); Molucca Ids. (ANSP; BMNH). PHILIPPINE IDS.: Sindangan Bay, Dapitan, Iligan Bay, Lupon, Davao Province, all Mindanao; Lampinegan Island, off Basilon; Apari, north Luzon (all USNM). SOLOMON IDS.: Lunga, Guadalcanal (USNM). FIJI IDS.: off Rukua, Mbega Id. (USNM).

Tellina (Tellinides) natalensis Philippi
Plate 11, figure 2; Plate 12, figures 3, 4; Plate 13, figure 3.

Tellina natalensis (Krauss MS) Philippi 1846, Abbild. Beschreib. Conch., 2: 91, *Tellina*, pl. 4, fig. 4 (no locality given); Krauss 1848, Die südafrikanischen Mollusken, p. 3 (type-locality, in litore natalensi; holotype, ? Stuttgart).[1]

Description. Shell extending to 24 mm in length and to 14 mm in height, subrectangular to subelliptical, inequilateral, nearly equivalve, subsolid, somewhat compressed, and with slight posterior flexure to right. Umbo behind middle, small, not conspicuous, opisthogyrous, pointed, compressed, not elevated or inflated, but with moderately deep cavity. Anterior margin rather narrowly and smoothly rounded; ventral margin slightly convex, rising with slightly indented arcuation behind; anterior dorsal margin long, very gently sloping; posterior dorsal margin short, straight to weakly concave; posterior margin variable, irregularly and obliquely truncated, giving outline pointed or bluntly truncated appearance. Sculpture consisting of finely incised sulcations, generally becoming obscure on posterior portion of disc and slope; umbonal concentric sculpture lirate and intercalated posteriorly; radial sculpture obsolete. Posterior ridge weak and gentle.

Ligament short, yellow to brownish black, and set upon variously developed nymphal callosities; escutcheon and lunule obsolete. Hinge line weakly developed. In left valve, cardinal complex consisting of anterior, narrow bifid tooth with subequal lobes, and of flat, shelf-like laminate posterior tooth closely adpressed to base of nymphal callosity; no lateral teeth developed. In right valve, cardinal complex consisting of small, posteriorly skewed, posterior bifid tooth with anterior lobe smaller, and of anterior, slightly thickened, laminate tooth; no true posterior lateral tooth; anterior lateral tooth small, rounded, blunt,

[1] The type-specimens of the species described by Krauss were probably destroyed in World War II (Dance, 1966).

peglike, and very closely juxtaposed to anterior cardinal tooth.

Muscle scars rather weakly impressed. Anterior adductor muscle rounded ventrally, irregularly semilunate; posterior adductor muscle irregularly rounded to subquadrate; retractor scar evident. Pallial sinus rising sharply posteriorly, pointed apex beneath umbo, more or less straight and steeply descending centrally, rounded and arcuate anteriorly, but well separated from anterior adductor muscle scar and confluent with pallial line for about two thirds of its ventral length. Cruciform muscle scars variously impressed, rounded, except for subrectangular right anterior scar, and close to ventral margin. Shell white, pink, or red, and combinations thereof; often rayed in white posteriorly; generally shining and polished internally with radial vermiculations.

Length mm	Height mm	Width mm	
23.8	13.3	—	Durban
19.1	10.5	05.0	Durban
17.1	09.1	04.0	Durban
14.2	08.2	03.8	Durban
07.6	03.9	02.1	Durban

Remarks. Tellina natalensis exhibits a considerable range of variation in the shape of the posterior portion of its shell. The length of the posterior dorsal margin and its angle of obliquity determine the posterior outline or aspect of the shell. Most individuals are broadly truncate with a slightly inclined and relatively short posterior margin, but not infrequently some individuals have the posterior dorsal and posterior margins nearly coextensive, in which case the shell is pointed behind and the truncation rather sharply angular.

The shell in *T. natalensis* is usually rather highly colored with red or pink and may be rayed posteriorly. Some iridescence is exhibited, due generally to the finely incised sulcations, which are slightly acentric peripherally and which disappear on the posterior quarter of the disc.

The relationships of this species to other South African tellens are obscured by the current concepts of the generic and subgeneric groups within the Tellinidae. The small tellens, i.e. *T. prismatica, T. vidalensis,* and *T. gilchristi,* are most easily confused with *T. natalensis.* The key distinguishing traits of *T. natalensis* are illustrated on Plate 12, figures 3 and 4, including the structure of the dentition of the right valve and the configuration of the pallial sinus in both valves. The sinus does not coalesce with the anterior adductor muscle scar and is really quite widely separated from it. Further, in *T. natalensis,* the right anterior lateral tooth is very closely juxtaposed if not virtually coextensive with the anterior laminate tooth of the cardinal complex.

I have placed *T. natalensis* in *Tellinides* because it shares so many common characters with that group and is apparently most closely related (in South African waters) to *T. opalina.* First, *T. natalensis* has the centrally placed peglike right anterior lateral tooth and the tendency to be posteriorly rayed along the growth axis of the cruciform muscle scars. In addition, the pallial scars of both species are quite similar, particularly in regard to the shape of the sinus and its angle of ascent from the base of the posterior adductor muscle scar. The species are distinguished most easily by the shape of the shell and the location of the umbo.

The specimens referred to as *T. scalpellum* Hanley by Day and Morgans (1956), and later referred to as *T. natalensis* by Barnard (1964b), have a strong right anterior lateral tooth some distance removed from the cardinal complex and are not *T. natalensis* but *T. prismatica* (*q.v.*).

In the description of *T. natalensis,* Barnard (1964b) spoke of the three cardinal teeth of the right valve. In the present interpretation, the anteriormost of these teeth is considered an anterior lateral tooth.

Range. Smith (1904) reported this species from Port Alfred, although it prob-

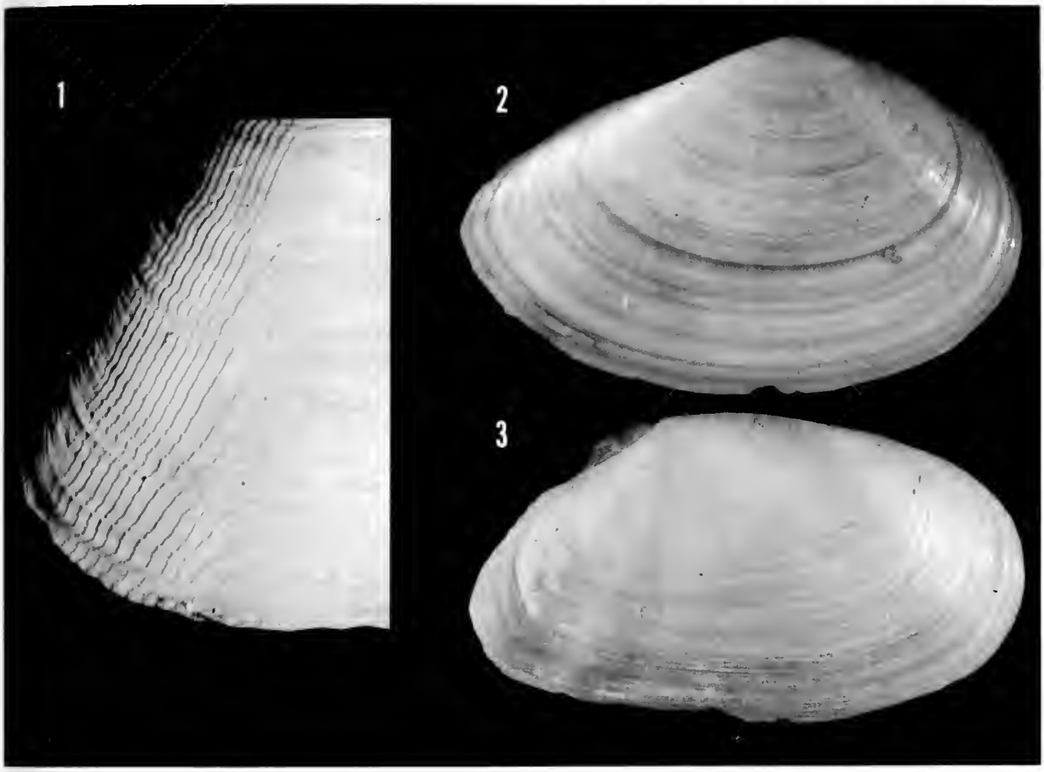


Plate 13. Figs. 1 and 2. *Tellina* (*Homalina*) *trilatera* Gmelin, Muizenberg, False Bay, South Africa, USNM 623580 (length = 31.2 mm): Fig. 1, enlargement of the posterior slope of the right valve to show acentric sculpture; Fig. 2, external view of the right valve. Fig. 3. *Tellina* (*Tellinides*) *natalensis* Philippi: external view of the right valve, Durban, SAM A7637 (length = 14.2 mm).

ably lives only in the warm waters of east Africa as far south as Durban.

Specimens examined. REPUBLIC OF SOUTH AFRICA: Durban (DN; NM; SAM). MOZAMBIQUE: Morrumbene Estuary (UCT).

Subgenus *Homalina* Stoliczka

Homalina Stoliczka 1870, Cretaceous Fauna of Southern India, 3: 118 (type-species, *Tellina triangularis* (Chemnitz) Röding 1798 [= *Tellina trilatera* Gmelin 1791], original designation).

Description. Shell medium in size, generally subtrigonal in shape, compressed, inequilateral. Umbos anterior, slightly elevated, with cavities. Ligament moderate, protuberant. Dentition rather weak; cardinal teeth normal; right anterior lateral tooth very closely adjacent to the cardinal complex. Pallial sinus usually extensive, sometimes coalescent with anterior adductor muscle scar. Color generally white with polished periostracum.

Remarks. Mörch (1853) used a "*Homala* Schumacher," which was an unnecessary emendation for *Omala* Schumacher 1817. He included *T. triangularis* (Chemnitz) Röding 1798 [= *T. trilatera* Gmelin] and three synonyms. This is apparently just Mörch's placement of *T. trilatera* in '*Homala*.' *Homala* was truly introduced as an emendation for *Omala* Schumacher 1817 by Agassiz (1846: 258). But it is not only unnecessary, it is useless, since it is preoccupied by *Homala* Eschscholtz 1831. *Omala* Schumacher is monotypic and the correct subgeneric name for *T. hyalina*.

The relationship between the monotypic

Omala and *Homalina* becomes immediately obvious when the respective type-species for these subgenera (the West African *T. hyalina* Gmelin and the South African *T. trilatera* Gmelin) are compared. The shells of these species are similar in having an anterior placement of the umbo. Both have a very small to obsolete right anterior lateral tooth virtually incorporated into the cardinal complex. In shell structure they have similar sculpture, texture, thickness, and color. I have treated *Homalina* separately—that is, I have not synonymized it with *Omala*—because *T. hyalina* is so obviously unique. No other tellen has the umbo placed so far anteriorly, the peculiarly elliptical outline of the valves, or the inset ligament with a flange on the posterior dorsal margin.

Homalina is also very similar to *Tellinides.* Yet there is some justification for maintaining a separate status for these groups, in as much as *Homalina* is characterized by species that are distinctly subtrigonal and whose right anterior lateral tooth is almost coalescent with the cardinal complex. *Homalina* is represented in New Zealand by the large, posteriorly pointed, and transversely trigonal *T. gaimardi* Iredale. Another trigonal group—in the Australian-New Zealand region—is *Macomona*, with the New Zealand *T. liliana* Iredale as type, and with *T. tristis* Deshayes and three other species in New South Wales in Australia (Iredale and McMichael, 1962). *Macomona* is certainly more distantly related to *Homalina* and is distinguished by its very strong subproximal anterior lateral tooth, its thickened, heavy shell, its sharp posterior flexure, and an extensive semilunate anterior adductor muscle.

Tellina (Homalina) trilatera Gmelin
Plate 10, figure 4; Plate 13, figures 1, 2; Plate 14, figure 2.

Tellina trilatera Gmelin 1791,[1] Syst. Nat., ed. 13, p. 3234 (type-locality not given, here restricted to Port Alfred, Republic of South Africa; holotype, ? Zoological Museum, Copenhagen; refers to Chemnitz 1782, Conch.-Cab., vol. 6, p. 96, pl. 10, fig. 85).

Tellina strigilata Spengler 1798. Skrivter af naturhistorie Selskabet, København, 4 (2): 98 (type-locality, Fra Kysten Guinea, here corrected and restricted to Port Alfred, Republic of South Africa; holotype, ? Zoological Museum, Copenhagen; refers to Chemnitz 1782, Conch.-Cab., vol. 6, p. 96, pl. 10, fig. 85).

Tellina triangularis Röding 1798, Mus. Bolt., p. 188 (type-locality not given, here restricted to Port Alfred, Republic of South Africa; holotype, ? Zoological Museum, Copenhagen; refers to Chemnitz 1782, Conch.-Cab., vol. 6, p. 96, pl. 10, fig. 85), *non* Gmelin 1791.

Tellinides politus Sowerby 1825, Catalogue . . . Tankerville, Append., p. 4 (type-locality, not given, here restricted to Port Alfred, Republic of South Africa; type not known[2]).

Description. Shell extending to 47 mm in length and to 33 mm in height, subtrigonal, inequilateral, thin to subsolid, compressed, with right valve slightly more convex than left, and with very slight flexure to right posteriorly. Umbos well in front of middle, small, pointed, smooth, and slightly inflated. Anterior margin broadly rounded and of irregular convexity; ventral margin gently convex, extensive, rising convexly posteriorly; anterior dorsal margin short, convex, and gently descending; posterior dorsal margin more sharply descending, elongate, and more or less straight; posterior margin indistinct and short, forming pointed, subacuminate outline. Sculpture consisting of extremely fine, weak, concentric lirations somewhat stronger on posterior dorsal slope; periostracum with finely incised subconcentric sulci; fine radial sulci evident on posterior slope in right valve. Posterior radial ridge in right valve, setting off dorsal posterior

[1] First referred to in the non-binomial Chemnitz (1782) as *T. triangularis*; the locality was originally unknown: "Das wahre Vaterland derselben ist mir unbekannt." Next mention of the species, but not named except for the common epithet "Die dreyseitige Telline" was Schröter (1786: 3).

[2] This name is included following its citation by Mörch (1853: 11) and Römer (1872: 180). The short Latin description certainly applies to *T. trilatera.* To my knowledge *politus* was never figured.

flattened area; weak concomitant ridge and sulcus in left valve.

Ligament black-brown, moderately strong, slightly protuberant and set in lanceolate escutcheon; no true lunule. Calcareous portion of ligament subtended by flattened nymphs. Hinge line rather weakly developed. In left valve, cardinal complex consisting of anterior, narrow, protuberant bifid tooth with subequal lobe, and of posterior, very thin, oblique laminate tooth, adpressed and partly coalesced with base of nymphs, often lost, broken or obscure; slight distal thickening of hinge line representing obsolescent posterior lateral tooth, and anterior lateral tooth closely proximal to cardinal complex, laminate and arcuate. In right valve, cardinal complex consisting of posterior, oblique, narrow, bifid tooth with subequal lobes, and of anterior, narrow, laminate tooth; posterior lateral tooth distal, thin, weakly pointed, slightly upcurled and socketed above; anterior lateral tooth immediately anterior to laminate cardinal tooth and often partially coalescent, thin, shelf-like and bluntly pointed.

Muscle scars rather weakly impressed. Anterior adductor muscle scar rounded anteriorly, flattened ventrally, and subsemilunate; posterior adductor muscle scar subtrigonal to subquadrate. Pallial sinus unequal in opposite valves. In right valve, pallial sinus descending in more or less straight line from posterior adductor muscle scar to point separated from anterior adductor scar and above pallial line, then falling in short, straight line to pallial line; confluence over 3/4 ventral length of pallial line. In left valve, pallial sinus extending more or less straight from base of posterior adductor muscle scar directly across interior of valve to unite with anterior adductor muscle scar; confluence entire. Cruciform muscle scars difficult to discern, rounded, closely juxtaposed, and with internal radial vermiculations or weak riblets marking their attachment. Shell white, covered externally with pale yellowish green periostracum, usually partially eroded; rust discolorations often evident on posterior dorsal slope; internally white, weakly polished.

Length mm	Height mm	Width mm	
46.6	32.7	—	Jeffrey's Bay
44.2	31.8	—	Hout's Bay
42.3	28.9	09.5	Muizenberg, False Bay
30.6	21.2	07.8	Durban Bay
29.0	20.4	07.0	Durban Bay
26.4	17.7	05.8	Muizenberg, False Bay

Remarks. The occurrence of this species in South Africa was recognized by von Martens (1874). Specimens from Saldanha Bay taken at a depth of 6.5 m in a substrate of fine white sand and grey mud were found to have the posterior slope of the valves discolored (probably by some iron compound in the substrate). The discoloration is present on both valves but more extensively on the right. Small epizoic organisms were found on several individuals. Their greatest concentration is on the posterior slope of the right valve. From these facts, it is apparent that the species lives in the substrate on its left side just below the surface, at an angle which allows a slight protrusion of the posterior part of the valves out of the substrate.

The closest relative of *T. trilatera* is *T. gaimardi* Iredale 1915 (= *T. alba* Quoy and Gaimard 1835, *non* Wood 1815) from New Zealand. The similarity in shape, the structure of the hinge, and the kind of dentition indicate the close relationship between these species. *T. gaimardi* has no flattened posterior dorsal slope and attains a larger size. In the left valve of *T. gaimardi*, the pallial sinus does not coalesce with the anterior adductor muscle scar as it does in *T. trilatera*.

Barnard (1962b) has listed the occurrences of this species in the fossil record in South Africa. It has been found as far north as Port Nolloth, Little Namaqualand (Haughton, 1932) and as far east as Knysna.

Range. Tellina trilatera is exclusively South African and occurs in shallow coastal

waters in fine sandy or muddy substrates from South West Africa to Durban Bay. Recently, Grindley and Kensley (1966) obtained it off the mouth of the Orange River, South West Africa.

Specimens examined. REPUBLIC OF SOUTH AFRICA: Saldanha Bay (MCZ; UCT); Langebaan Lagoon, Saldanha Bay (UCT); Hoedjies, Saldanha Bay (ANSP); Hout's Bay (NM); Cape of Good Hope (MCZ); False Bay (NM; UCT); Muizenberg, False Bay (USNM); Satt Vlei Beach, Hermanus, Klein River (ANSP); Still Bay (SAM); Plettenberg Bay (MCZ); Humansdorp Coast, Jeffrey's Bay (SNM); Albany (USNM); Port Alfred, near Grahamstown (USNM); Port Alfred, Bathurst District (BMNH; MCZ); Natal (BMNH); Durban Bay (DM).

Subgenus *Cadella* Dall, Bartsch and Rehder

Cadella Dall, Bartsch and Rehder 1938, Bishop Museum, Bull., 153: 196 (type-species, *Tellina lechiogramma* Melvill 1893, original designation).

Description. Shell small, solid, and ovate-subelliptical. Umbos behind middle, opisthogyrous and blunt. Sculpture consisting of rather strong, closely spaced lirations. Ligament short, strong, and sunken in escutcheon; small subumbonal internal ligamental element sometimes developed. Pallial sinus extending close to anterior adductor muscle scar, sharply descending, and forming short confluence with pallial line posteriorly.

Remarks. Dall, Bartsch, and Rehder (1938) have given a long description for this group. Its affinities are clearly with *Moerella,* but it apparently is distinct in its heavy strong shell and its concomitantly thickened hinge line and strong lateral teeth. The Caribbean *Acorylus* Olsson and Harbison 1953 (with *Tellina suberis* Dall 1900 as type-species and with *T. gouldii* Hanley 1846 as a living representative) differs in its smooth sculpture and its pallial sinus, which is basally confluent with the anterior adductor muscle scar. *Elliptotellina* Cossmann 1886 (type-species *Donax tellinella* Lamarck 1805) is also related to *Cadella.* However, species of *Elliptotellina,* for example, *T. fabrefacta* Pilsbry in the Indo-Pacific, are variously sculptured radially along the posterior surfaces of the valves and are, by and large, equilateral, with the umbos nearly always centrally placed. The tiny subumbonal internal ligament of *Cadella* is similar to the conspicuous, developed internal ligament of the semelid group, *Semelangulus.* Apparently this condition is convergent.

Tellina (*Cadella*) *semen* Hanley
Plate 14, figure 5; Plate 15, figures 1–4.

Tellina semen Hanley 1844, Proc. Zool. Soc. London [1845], pt. 12, no. 141: 164 (type-locality, Corregidor [Philippine Islands]; types not known, not in type collection in BMNH; 1846 [*in*] Sowerby, Thes. Conch., vol. 1, *Tellina,* p. 249, pl. 56, fig. 8; Sowerby 1867 [*in*] Reeve, Conch. Icon., vol. 17, *Tellina,* pl. 41, fig. 232.

Tellina fabagella Deshayes 1854, Proc. Zool. Soc. London [1855], pt. 22, no. 174: 355 (type-locality, Albay Islands of Luzon, Philippine Islands; syntypes, BMNH unnumbered).

Tellina semitorta Sowerby 1867 [*in*] Reeve, Conch. Icon., vol. 17, *Tellina,* pl. 39, figs. 221 a-b (type-locality, Watson's Bay, Port Jackson, New South Wales, Australia; syntypes, BMNH 70.10.26.17).

Tellina striatissima Sowerby 1868 [*in*] Reeve, Conch. Icon., vol. 17, *Tellina,* pl. 45, fig. 226 (type-locality not given; holotype, BMNH 1900.3.9.13).

Tellina miracyllium Melvill and Standen 1906, Proc. Zool. Soc. London [1907], 2 (4): 820, pl. 56, fig. 4 (type-locality, Koweit [*sic*], Persian Gulf; holotype, BMNH 1907.5.3.87).

Tellina europisthus Barnard 1964, Ann. Natal Mus., 16: 27, fig. 5 c (type-locality, off Cape Natal, Durban, in 54 fathoms; syntypes, SAM A 9549).

Description. Shell extending to 12 mm in length and to 9 mm in height, subelliptical-subovate, inequilateral, equivalve, solid, inflated, and with slight posterior flexure. Umbos behind middle, inflated, little elevated, and blunt. Anterior margin narrowly and smoothly rounded; ventral margin gently convex, rising in regular arcuation posteriorly; anterior dorsal margin long, gently descending, and generally

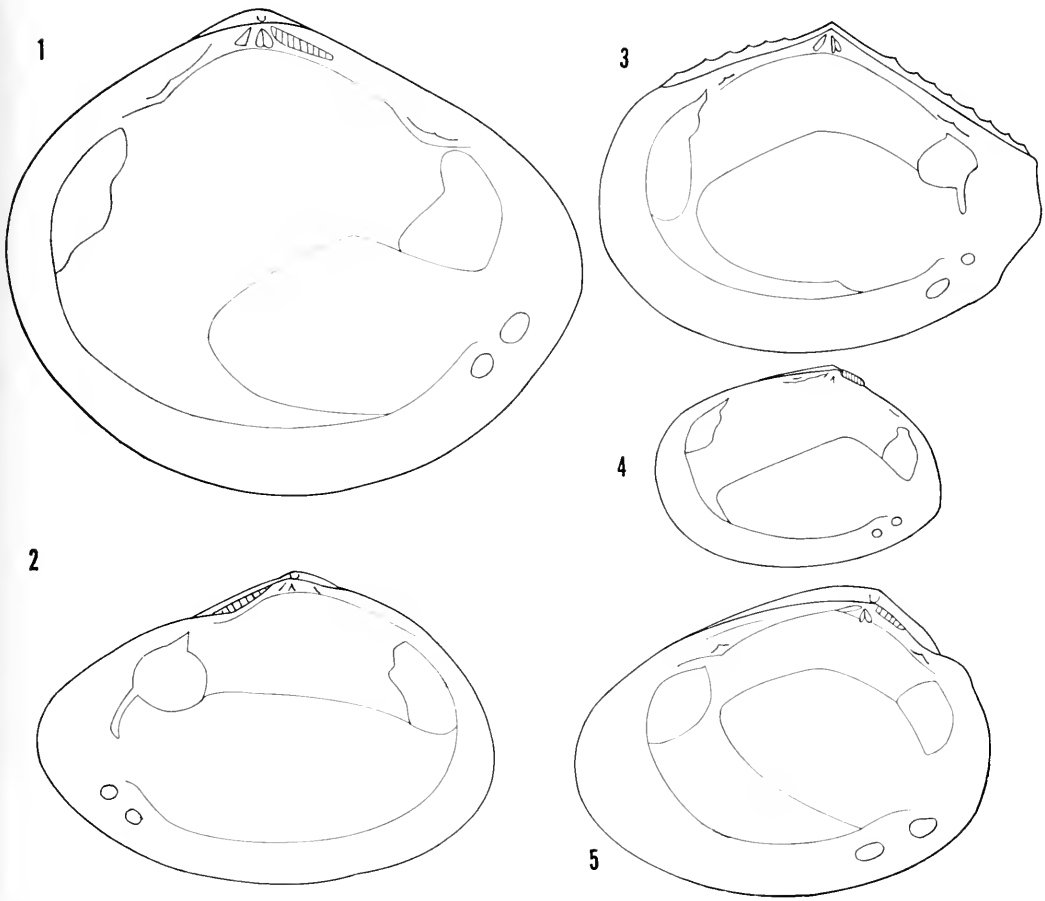


Plate 14. Diagrammatic illustrations of the internal surface of the valves, showing the dental configuration and muscle scars. Fig. 1. *Tellina (Arcopagia) ponsonbyi* Sowerby: right valve, Albany, South Africa, USNM 98045 (length = 21.5 mm). Fig. 2. *Tellina (Homalina) trilatera* Gmelin: left valve, Langebaan Lagoon, Saldanha Bay, South Africa, UCT-LB 63 (length = 18 mm). Fig. 3. *Tellina (Serratina) capsoides* Lamarck: right valve of young individual, Durban, DM 3650 (length = 17 mm). Fig. 4. *Tellina (Angulus) canonica* Salisbury: right valve, Still Bay, South Africa, SAM A30019 (length = 11 mm). Fig. 5. *Tellina (Cadella) semen* Hanley: right valve, Delagoa Bay, Mozambique, SAM A9552 (length = 8.8 mm).

straight; posterior dorsal margin short, steeply descending, and generally straight; posterior margin weakly convex and forming bluntly rounded truncation. Sculpture consisting of closely spaced, raised, concentric lirations (7–9 per mm on the disc); no true radial sculpture. Concentric lirations sublamellate and intercalated along posterior slope, particularly in right valve. Broad radial depression along posterior slope in left valve; no defined posterior ridges developed.

Ligament yellow to brown, opisthodetic, short, slightly protuberant, and sunken in depressed short escutcheon; secondary, inconspicuous, subumbonal resilium element sometimes developed. Calcareous portion of ligament subtended by strong hinge line, but elevated nymphal callosity hardly developed. Elongate, lanceolate lunule present, stronger in left valve, defined by anterior dorsal marginal ridge. Hinge line well developed. In left valve, cardinal complex consisting of anterior subdeltoid

bifid tooth with subequal lobes and of elongate sublaminate tooth often coalesced with base of nymphs or broken; lateral dentition narrow, flattened, and pointed; anterior tooth far removed and posterior tooth subproximal to cardinal complex. In right valve, cardinal complex consisting of posterior strong subdeltoid bifid tooth with posterior lobe larger and skewed posteriorly and of anterior sturdy sublaminate tooth; lateral dentition strong, heavy, socketed above, and pointed; anterior lateral distal and posterior lateral subproximal to cardinal complex.

Muscle scars moderately or poorly impressed. Anterior adductor scar elongate-rounded; posterior adductor subquadrate-rounded; pallial sinus equal in both valves, rising gently, narrowly rounded anteriorly, sharply descending and forming short confluence with pallial sinus posteriorly. Pallial sinus extending very close to anterior adductor muscle scar along its dorsal arcuation. Cruciform muscle scars difficult to discern, closely juxtaposed, rounded to somewhat flattened. Shell generally white; internal surface polished; external surface dull, often dirty white to yellowish brown; some yellow suffusions internally and occasionally reddish concentrations along hinge line.

Length mm	Height mm	Width mm	
11.8	08.5	05.5	Durban
10.2	07.2	04.5	Durban
09.5	06.5	—	syntype of *europisthus*
09.1	06.2	03.8	Mekran Coast
08.0	05.6	03.6	Delagoa Bay
07.3	05.2	—	syntype of *europisthus*

Remarks. Tellina semen is a widely distributed Indo-Pacific species. It exhibits a considerable range of variation, particularly in regard to its shape and its sculpture on the posterior dorsal slope of the right valve. A number of the synonyms of this species have been established on the character of the outline of the valves. I do not hesitate to consider *T. semitorta* a synonym of *T. semen*, though both Smith (1885) and Lynge (1909) treated each separately. Smith noted that *semen* and *semitorta* were closely allied but stated that *semen* was more elongate; he also noted that *semitorta* had some reddish coloration along the hinge line. Lynge showed that the populations that he referred to *semitorta* in the Gulf of Siam possessed no red coloration and were extremely variable in form. Comparison of specimens throughout the Indo-Pacific region, from Natal, South Africa, to the Fiji Islands, indicates that there are no consistent differences between isolated populations that would merit interpretation of any of these populations as distinct species or even subspecies. By any means, the populations referred to *T. semen* and *T. semitorta* by Smith and Lynge were sympatric.

The synonyms *miracyllium* Melvill and Standen, *striatissima* Sowerby, *fabagella* Deshayes, *europisthus* Barnard, and *semitorta* Sowerby have been established upon examination of type-material. Salisbury (1934) had already suggested that *miracyllium* and *striatissima* were synonymous with *semen*. The status of *semen*, the type-material of which cannot be located, is based upon the plates cited in the synonymy.

Tellina semen belongs to the subgenus *Cadella* Dall, Bartsch, and Rehder (1938). The concentric sculpture, the strong dentition of the right valve, and the configuration of the pallial sinus in *T. semen* are extremely similar to those of *T. lechiogramma* Melvill, the type-species of *Cadella*. In some respects *Cadella* is related to *Moerella* (type-species, *T. donacina* Linnaeus of European seas), but the pallial sinus in *Moerella* has a considerable coalescence with the pallial line, whereas in *Cadella* the sinus is confluent distally. Melvill and Standen (1907) and Lynge (1909) placed *T. semen* in *Moerella*.

One of the curious traits of *T. semen*, noted by Smith (1885), is the tendency of the resilial part of the ligament to form a separate, tiny, subumbonal portion. Although always inconspicuous, this feature

Plate 15. *Tellina* (*Cadella*) *semen* Hanley. Fig. 1. External view of the left valve, Durban, NM 1809 (length = 18 mm). Fig. 2. Internal view of the right valve, Durban, NM 1809 (length = 12.1 mm). Figs. 3 and 4. Syntype of *Tellina europisthus* Barnard [= *T. semen*], off Cape Natal, Durban, SAM 9549 (length = 8.5 mm): Fig. 3, external view of the right valve; Fig. 4, internal view of the right valve.

is variously developed, and in some specimens an extremely small chondrophore-like structure is evident. This morphological configuration indicates the relationship of the Tellinidae with the Semelidae; the latter normally have a larger conspicuous internal resilium supported by a well-developed chondrophore. Striking similarities are most evident between *Cadella* and the various species of the semelid genus *Semelangulus*, as noted by Dall, Bartsch, and Rehder (1938).

Another variable morphological characteristic exhibited in populations of *T. semen* is the nature of the concentric sculpture along the posterior slope in the right valve. Usually the concentric lirations become stronger, somewhat raised, and sublamellate. They are often reduced in number, becoming confluent with each other at various distances from the posterior margin. Such a pattern of intercalations of concentric lirations was chosen by Barnard (1964a) as the best distinguishing trait in his synonym *europisthus*.

Range. *Tellina semen* lives in offshore waters, usually in relatively coarse substrates from along the coast of east Africa as far south as Durban, through the East Indies and the Philippine Islands to as far east as the Fiji Islands. Smith (1903) first listed the species from Durban, and further documentation of range has been given by Lynge (1909). Under the name

semitorta, Maes (1967) noted that this species was abundant at Cocos-Keeling in fine, soft sand in shallow water. It was not an intertidal or beach species and rapidly buried itself in the substrate if disturbed. Odhner (1919) recorded this species as *semitorta* from Madagascar.

Specimens examined. REPUBLIC OF SOUTH AFRICA: Durban (BMNH; NM); Cape Natal (SAM); Morewood Cove (SAM); Tugela River, Zululand (SAM). MOZAMBIQUE: Delagoa Bay (SAM). SEYCHELLES IDS.: NW Mahe (BMNH). PERSIAN GULF: (BMNH). WEST PAKISTAN: Mekran Coast (BMNH; USNM); Karachi (BMNH). INDIA: Tuticorin, Gulf of Mannar (BMNH); Madras (BMNH). ANDAMAN IDS.: Port Blair (BMNH). MALAYSIA: Singapore: (BMNH). PHILIPPINE IDS.: (BMNH). AUSTRALIA: Flinders Passage and Cape York, Torres Straits (both BMNH). FIJI IDS.: (BMNH).

Subgenus *Moerella* Fischer

Donacilla Gray 1851, (British) Mollusca Acephala and Brachiopoda. List of the . . . British Animals in the . . . Museum, Part 7, p. 39 (type-species, *Tellina donacina* Linnaeus 1758, subsequent designation, Herrmannsen 1852, p. 47), *non* Lamarck 1819 (Mollusca).

Mocra H. and A. Adams 1856, Genera Recent Moll., 2: 396 (type-species, *Tellina donacina* Linnaeus 1758, subsequent designation, Kobelt 1881: 328), *non* Huebner 1819 (Lepidoptera), *nec* Milne-Edwards 1840 (Crustacea), *nec* Michelin 1855 (Echinodermata).[1]

Maera H. and A. Adams 1858, Genera Recent Moll., Index, p. xxvii, error for *Mocra* H. and A. Adams 1856, *non* Leach 1814 (Crustacea).

Moerella Fischer 1887, Manuel de Conch., p. 1147 (type-species, *Tellina donacina* Linnaeus 1758, monotypy).[2]

Description. Shell usually small, elongate-subelliptical, solid, somewhat inflated to compressed, inequilateral, and more or less equivalve, with posterior flexure to right. Umbos behind middle, low and opisthogyrous. Concentric sculpture consisting of more or less regularly spaced, strong, lirations, usually intercalated and sublamellate on right posterior slope. Hinge well developed. Right anterior and posterior lateral teeth strong and socketed above; anterior tooth subproximal to cardinal complex. Pallial sinus extending near to but separated from anterior adductor muscle scar and extensively confluent with pallial sinus posteriorly. Color often reddish with bands and/or rays.

Remarks. Moerella approaches *Cadella* in many respects. Yet the latter has a stronger, heavier, and thicker shell, with concomitantly stronger hinge teeth. In outline, *Moerella* tends to be somewhat pointed posteriorly, and its pallial sinus, largely confluent with the pallial line ventrally, extends close to the anterior adductor muscle scar. In addition, the right anterior lateral tooth of *Cadella* is thick, socketed above, and more distantly disposed in relation to the cardinal complex than is the homologous tooth in *Moerella,* which, though developed, tends to be shelf-like, upcurled, and more proximally juxtaposed to the cardinal complex.

Tellina donacina Linnaeus, the type-species of *Moerella,* lives in the Mediterranean Sea and the eastern Atlantic Ocean (Bucquoy, Dautzenberg, and Dollfus, 1887–98) and is very closely related to *T. vidalensis* of South Africa. Also in European waters, *T. pulchella* Lamarck is very similar to *T. gilchristi.* In the Americas, species such as *T. sybaritica* Dall, which I had once considered in *Angulus* (Boss, 1968), appear to belong to the *Moerella* complex. Nevertheless, the distinctions between *Angulus* and *Moerella* are tenuous.

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[1] The type-species is not *T. distorta* Poli 1795, as given by Salisbury 1934. (Actually, since *Mocra* is a replacement name for *Donacilla* Gray, *non* Lamarck, its type-species automatically becomes *T. donacina* so indicated by Herrmannsen for *Donacilla.* Stoliczka (1870) gave no designation.)

[2] Fischer does not state that he is giving a replacement name for *Mocra* H. and A. Adams 1856 [= *Donacilla* Gray 1851], for he does not indicate that it was preoccupied. Since he lists *T. donacina* as an example, we construe that as type-species by monotypy.

Tellina (Moerella) vidalensis Sowerby
Plate 16, figures 2–5; Plate 17, figures 1, 2.

Tellina vidalensis Sowerby 1904, Marine Investigations South Africa, 4: 13, pl. 7, fig. 5 (type-locality, Cape Vidal, NE by N, 9 miles, in 13 fathoms; holotype, SAM Reg. No. 14848).

Description. Shell extending to 19 mm in length and to 10 mm in height, elongate, sublanceolate, inequilateral, more or less equivalve, solid, right valve slightly more inflated with short, sharp flexure to right posteriorly. Umbo well behind middle, opisthogyrous, small, inconspicuous, not inflated or elevated, flattened, and with shallow cavity. Anterior margin smoothly and narrowly rounded; ventral margin weakly convex, rising in concave arcuation posteriorly; anterior dorsal margin very long, weakly convex to straight, and gently descending; posterior dorsal margin short, straight to weakly concave, and steeply descending; posterior margin short, irregularly convex, forming slight truncation and rather sharply pointed outline at junction with ventral margin. Sculpture consisting of incised, fine concentric lirations, intercalated and stronger along posterior dorsal slope; no true radial sculpture; lirations imparting silky, sheen-like appearance to external surface of valves. Posterior ridge in both valves weak and rounded.

Ligament short, yellowish brown to black, protuberant, and set in rather wide, lanceolate escutcheon; lunule indistinct, elongate, lanceolate, stronger in left valve. Hinge well developed. In left valve, cardinal complex consisting of anterior strong, deltoid bifid tooth with subequal lobes, and of posterior, thin, oblique laminate tooth; lateral teeth consisting of distal thickenings of hinge line. In right valve, cardinal complex consisting of anterior, strong, laminate tooth, and of posterior, somewhat skewed, subdeltoid bifid tooth with subequal lobes; anterior lateral tooth distal, strong, upcurled and shelf-like; posterior lateral tooth distal, blunt, and socketed above.

Muscle scars moderately well impressed. Anterior adductor scar rounded ventrally, irregularly semilunate; posterior adductor scar irregularly subquadrate. Pallial sinus equal in opposite valves, rising slightly posteriorly, gently pointed in apex beneath umbo, gently descending in straight or concave arcuation, rounded or sharply falling to pallial line anteriorly; not reaching anterior adductor muscle scar, and coalescent with pallial line for more than three-quarters its ventral length. Cruciform muscle scars closely juxtaposed, near ventral margin, and rounded except for subrectangular left anterior scar. Shell salmon pink, dark red, apricot or white; sometimes rayed or banded; internally shining, polished, and suffused with pink.

Length mm	Height mm	Width mm	
18.6	09.9	05.0	off Nonoti River, Natal
17.3	09.6	04.8	off Flat Rock, Natal
15.5	08.5	04.2	Holotype of *vidalensis*
10.4	05.2	02.4	off Flat Rock, Natal

Remarks. Tellina vidalensis is a rather heavily shelled species. It has regular lirate sculpture, which imparts a sheen-like appearance to the external surface of the valves. As illustrated in the figures, the concentric sculpture becomes stronger along the posterior dorsal slope.

The species is relatively easily distinguished from other small tellens in South Africa. *T. gilchristi* is more thinly shelled, with more pointed and conspicuous umbos; it has a longer posterior portion. *T. natalensis* is comparatively fragile, and its right anterior lateral tooth is closely juxtaposed to the cardinal complex, and *T. prismatica* has the pallial sinus coalescent with the anterior adductor muscle scar. In *T. vidalensis,* a left posterior lateral tooth is developed as a small, somewhat pointed, distal thickening of the hinge line posterior to the ligament.

Since the nature of the pallial sinus, the structure of the sculpture, and the form and strength of the shell are very similar, there is, no doubt, a relationship between

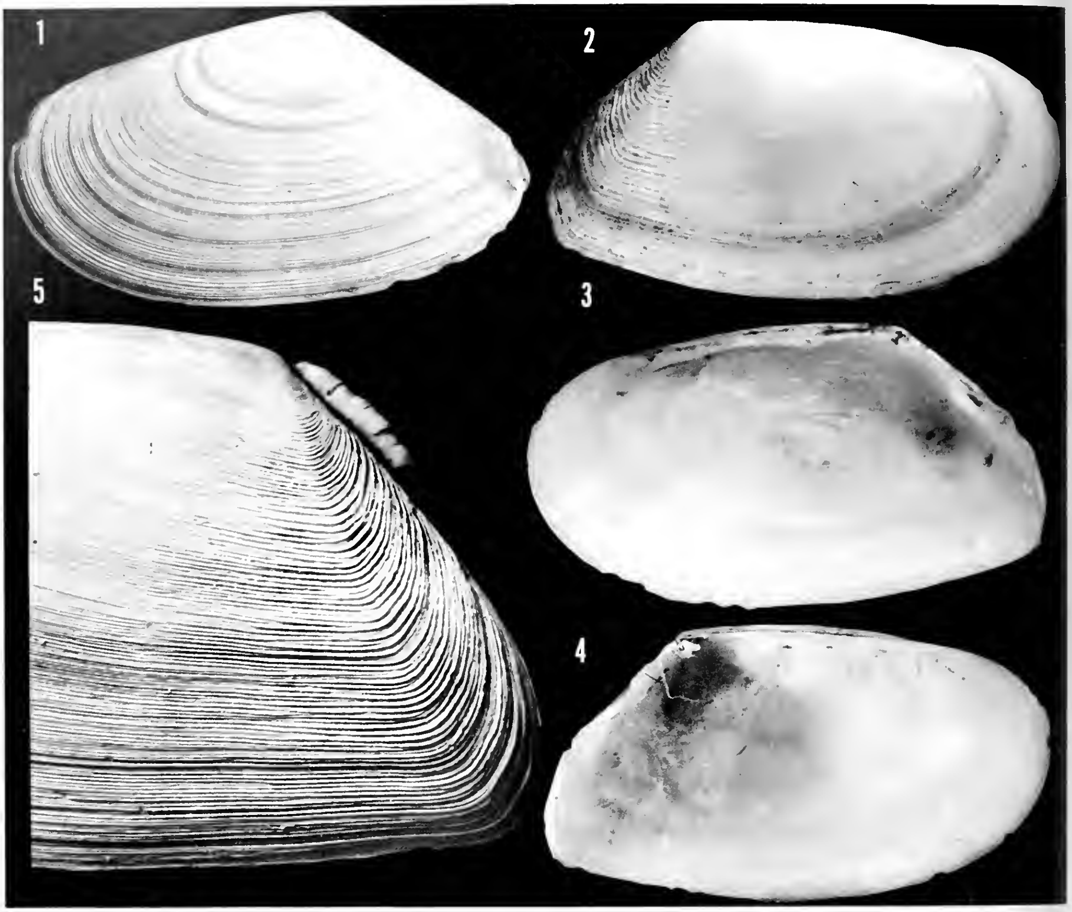

Plate 16. Fig. 1. Paratype of *Tellina* (*Moerella*) *gilchristi* Sowerby: external view of the left valve, showing strength of concentric lirations anteriorly, off Cape Point, South Africa, SAM 14751 (length = 24.8 mm). Figs. 2–4. Holotype of *Tellina* (*Moerella*) *vidalensis* Sowerby, off Cape Vidal, Zululand, SAM 14848 (length = 15.5 mm): Fig. 2, external view of the right valve; Fig. 3, internal view of the right valve; Fig. 4, internal view of the left valve, to show development of posterior lateral tooth. Fig. 5. *Tellina* (*Moerella*) *vidalensis* Sowerby: external surface of left valve to show strength of sculpture, off Nonoti River, Natal, UCT-63F (length = 13.5 mm).

T. donacina of European waters—the type-species of *Moerella*—and *T. vidalensis*. The former attains a slightly larger size, is less pointed posteriorly and somewhat higher in proportion, and its right anterior lateral tooth is closer to the cardinal complex.

As noted by Barnard (1964 b), the record of the occurrence of *T. vidalensis* at *Valdivia* Station 100 in Francis Bay (Thiele and Jaeckel, 1931) is questionable. However, the specimens collected by Stimpson in 1853 from False Bay, cited by Bartsch (1915), and referred to *T. gilchristi* by Barnard, are without doubt *T. vidalensis*.

The identity and status of many of these smaller tellens may remain a mystery for some time to come. I have no doubt that, for example, *T. vidalensis* is much more widely distributed in Indo-Pacific waters than the present record indicates. But larger series of specimens of small, shallow water species from widely different areas are not presently available. For example,

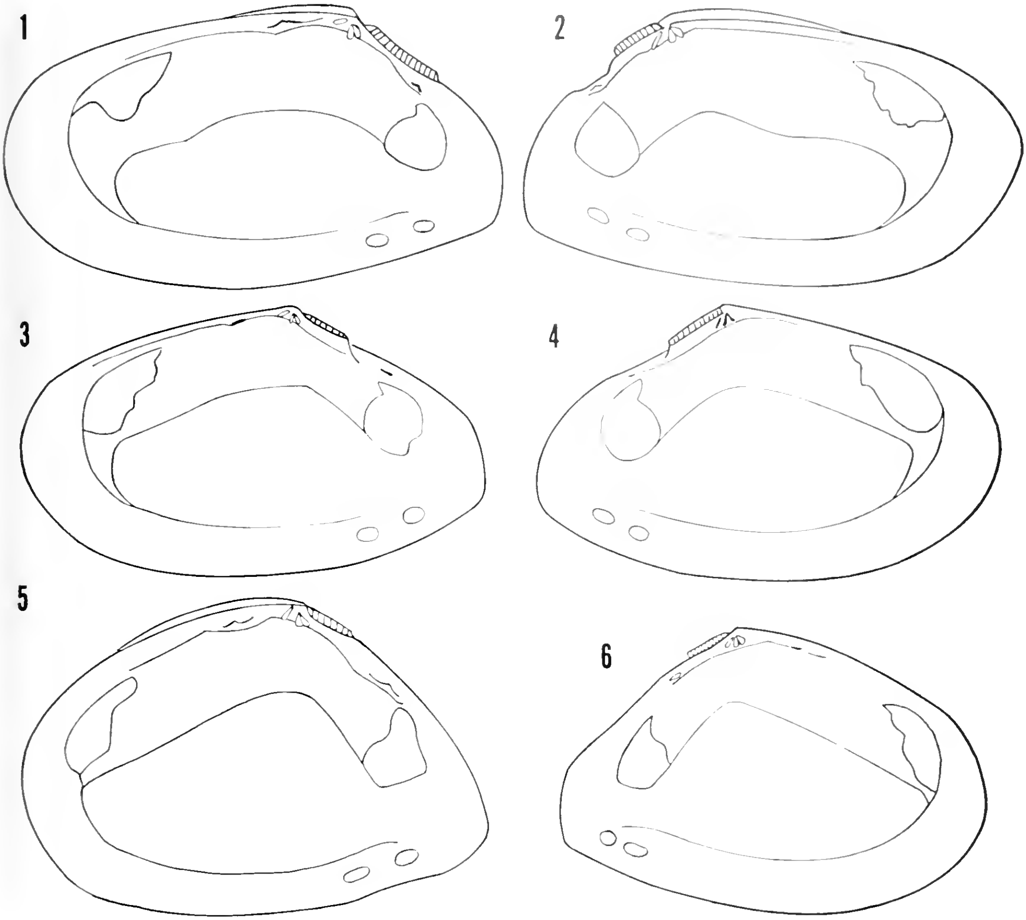

Plate 17. Diagrammatic illustrations of the internal surface of the valves, showing the dental configuration and muscle scars. Figs. 1 and 2. *Tellina* (*Maerella*) *vidalensis* Sowerby, off Cape Vidal, Zululand, SAM 14848 (length = 15.7 mm): Fig. 1, right valve; Fig. 2, left valve. Figs. 3 and 4. *Tellina* (*Maerella*) *gilchristi* Sowerby, off Kowie, South Africa, SAM 11491 (length = 14.6 mm): Fig. 3, right valve; Fig. 4, left valve. Figs. 5 and 6. *Tellina* (*Arcopagia*) *yemenensis* Melvill, Durban, DM: Fig. 5, right valve (length = 14.5 mm); Fig. 6, left valve (length = 13.5 mm).

in the Caribbean area, *T. sybaritica* Dall can hardly be separated from *T. vidalensis* of small size, yet *T. sybaritica* is usually thinner and never attains the overall size of adult *T. vidalensis*.

Range. *Tellina vidalensis* is predominantly an offshore warm water species found along the Natal and Zululand coast of South Africa in depths to 40 fathoms, in coarse sandy or muddy substrates.

Specimens examined. REPUBLIC OF SOUTH AFRICA: False Bay, Cape Province (USNM); off Umhlanga River in 22–26 fms.; off Umhloli River in 40 fms. (Barnard, 1964b); off Morewood Cove in 27 fms. (SAM); off Flat Rock in 57 m (29°19.1′S; 31°26.8′E); off Nonoti River in 38 m (29°21.6′S; 31°35.7′E) (both UCT); off Tugela River, Zululand, in 37 fms. (Barnard, 1964b); off Cape Vidal, near St. Lucia Bay, Zululand in 13 fms. (SAM).

Tellina (*Moerella*) *gilchristi* Sowerby
Plate 16, figure 1; Plate 17, figures 3, 4; Plate 18, figures 1, 2.

Tellina gilchristi Sowerby 1904, Marine Investigations South Africa, 4: 12, pl. 7, fig. 3 (type-locality, off Cape Point Lighthouse, NW by W, 11 3/4 miles, in 45 fathoms; holotype, BMNH 1904.12.23.156).

Tellina becki Turton 1932, The marine shells of Port Alfred, p. 247, pl. 66, no. 1741 (type-locality, Port Alfred; holotype, ? Oxford).

Description. Shell extending to 27 mm in length and to 16 mm in height, elongate-sublanceolate, inequilateral, equivalve, fragile to subsolid, rather compressed, with valves of near equal convexity and with a slight flexure to right posteriorly. Umbo behind middle, small, pointed, rather inconspicuous, and not elevated; umbonal cavity shallow. Anterior margin rather broadly and smoothly rounded; ventral margins slightly convex and rising behind; anterior dorsal margin long, straight, slightly convex, and gently descending; posterior dorsal margin short, rather steeply descending, and straight to slightly concave; posterior margin oblique, short, biangulate, and forming slightly pointed posterior outline. Sculpture consisting of finely incised concentric sulcations (about 8–12 per mm); intercalated lamellations present on posterior dorsal surface of each valve; sculpture stronger on right valve; no true radial sculpture. Posterior ridge slightly developed in right valve, ending at posterior ventral biangulation.

Ligament yellowish brown in color, rather strong, protuberant, weakly set in indistinct, sublanceolate escutcheon; no true lunule present; calcareous portion of ligament subtended by variously developed nymphal callosity, stronger in right valve. Hinge line moderately well developed. In left valve, cardinal complex consisting of anterior, narrow, bifid tooth with subequal lobes, and of elongate, posterior, thin laminate tooth; anterior lateral tooth obsolete, consisting of subproximal thickening of hinge line; posterior lateral tooth small, shelf-like, short, and pointed laterally. In right valve, cardinal complex consisting of posterior, narrow, bifid tooth, subequal lobes, and of anterior small, relatively thin, subdeltoid tooth; anterior lateral tooth subproximal to cardinal complex, elongate, shelf-like, thin, socketed above, and upcurled; posterior lateral tooth, distal, shelf-like, narrow, pointed, socketed above, and upcurled.

Muscle scars moderately well impressed. Posterior adductor scar irregularly subrectangulate; anterior adductor muscle scar irregularly semilunate. Pallial sinus equal in both valves, rising gently behind, apex pointed, gently descending anteriorly, forming a concave arcuation ventrally before uniting with pallial line. Pallial sinus well separated from anterior adductor muscle scar. Cruciform muscle scars rounded except for right anterior rectangular scar. Color basically white, suffused or banded with red or pink.

Length mm	Height mm	Width mm	
27.0	15.5	06.0	(Barnard)
24.8	14.3	05.5	Cape Point
18.7	10.1	04.0	False Bay
15.7	08.5	03.2	False Bay
13.2	08.8	02.9	off Kowie
10.1	05.5	02.1	False Bay
08.9	05.0	01.8	False Bay

Remarks. Probably the greatest variation exhibited by this species is its color pattern. The reds or pinks vary in intensity and they may be arranged in rays or bands. Rarely pure white individuals occur. The incised sculpture of the disc may be replaced by raised intercalated lirations on the posterior slope—particularly in the right valve.

The South African species that is most closely related to *T. gilchristi* is *T. analogica.* The former is distinct in its proportionately more narrow and elongate form, in its tendency to be somewhat pointed posteriorly rather than broadly and obliquely truncated, and in its usual red-pink coloration.

The species apparently occurs in considerable abundance in False Bay (Bar-

nard, 1964b; Dell, 1964). The University of Cape Town's Ecological Survey took the species at numerous stations in the Bay; living individuals were always found in depths beyond 10 m and most often occurred in fine green or khaki sands with some shell inclusions. It has been taken alive in depths of at least 87 m.

T. gilchristi is very closely related to *T. pulchella* from the Mediterranean. However, the latter is more elongate and pointed behind and attains a greater maximum size.

The West African *T. rubicincta* Römer[1] is very closely related to *T. gilchristi.* Nicklès (1955) cites the West African literature, lists a number of stations at which *rubicincta* occurs, and gives as its range, Mauritania to Angola. Not enough material from west Africa was available for study and I have seen no specimens of *gilchristi* from north of St. Helena Bay, in which case there may be a complete geographical separation of *gilchristi* and *rubicincta.* There is some indication that *rubicincta* is more tumid and more strongly sculptured on the right posterior dorsal slope than *gilchristi.*

Barnard (1964b) thought that the specimen collected by Stimpson in 1853 and referred to as *T. vidalensis* by Bartsch (1915) was really *T. gilchristi.* This specimen (USNM no. 66), from False Bay, Cape of Good Hope, is truly *T. vidalensis* (*q.v.*).

Range. T. gilchristi is found in the cool waters of South Africa from St. Helena Bay to off Port Alfred. Thiele and Jaeckel's (1931) record from Great Fish Bay, Angola, extends its range north, though I have not seen the VALDIVIA specimens. Boshoff's record (1965) from the north point lighthouse (Farol) at Inhaca, Mozambique, is doubtful.

Specimens examined. REPUBLIC OF SOUTH AFRICA: St. Helena Bay, in 69 m (UCT); Saldanha Bay, in 16 m (UCT); Langebaan Lagoon, Saldanha Bay (UCT); off Duyker Point, in 84 m (UCT); Buffels Bay (SAM); off Green Point (SAM); off Cape Point (SAM); False Bay, in 33–84 m (UCT); off Cape Infanta, St. Sebastian Bay (UCT); Aguilhas Bank (MCZ); off Cape St. Blaize, Mossel Bay (SAM); St. Francis Bay; Algoa Bay; off False Island and Nanquas Peak, Algoa Bay (after Barnard, 1964b); off Kowie or Port Alfred (MCZ; SAM).

Tellina (*Moerella*) *analogica* Sowerby
Plate 18, figures 3, 4; Plate 19, figure 1.

Tellina analogica Sowerby 1904, Marine Investigations South Africa, 4: 12, pl. 7, fig. 4 (type-locality, Constable Hill (Saldanha Bay) SE by E, 10 miles; holotype, not known).

Description. Shell extending to 22 mm in length and to 15 mm in height, subtrigonal to subrectangular, subsolid, inequilateral, nearly equivalve, with left valve slightly more convex and with posterior flexure to right. Umbos behind middle, small, not conspicuous, bluntly pointed, and opisthogyrous. Anterior margin somewhat narrowly rounded and convex; ventral margin straight to weakly convex, rising slightly posteriorly; anterior dorsal margin long, gently descending, more or less straight; posterior dorsal margin short, straight, and steeply descending; posterior margin usually biangulate, short, forming irregularly steep, blunt truncation. Sculpture consisting of fine, incised, concentric lirations and of extremely fine, radial vermiculations; concentric growth lines evident. Posterior ridge weak, extending to basal junction of posterior and ventral margins.

Ligament yellow-brown, moderately well developed, short, protuberant, set upon

[1] Römer's (1870: 32) spelling *rubicincta* is herein construed as the next available synonym for Gould's *rubicunda.* The references of Tomlin and Shackleford (1915) and Salisbury (1934) to a "*rubicincta* Gould 1845" are unfounded. The correct citation is: *Tellina rubicunda* Gould 1845, Proc. Boston Soc. Nat. Hist., 2: 37 (type-locality, Liberia; holotype, MCZ 169346); 1862, Otia Conch., p. 196; Johnson 1964, Bull. U. S. Nat. Mus., 239: 142, pl. 24, fig. 4, *non* Röding 1798.

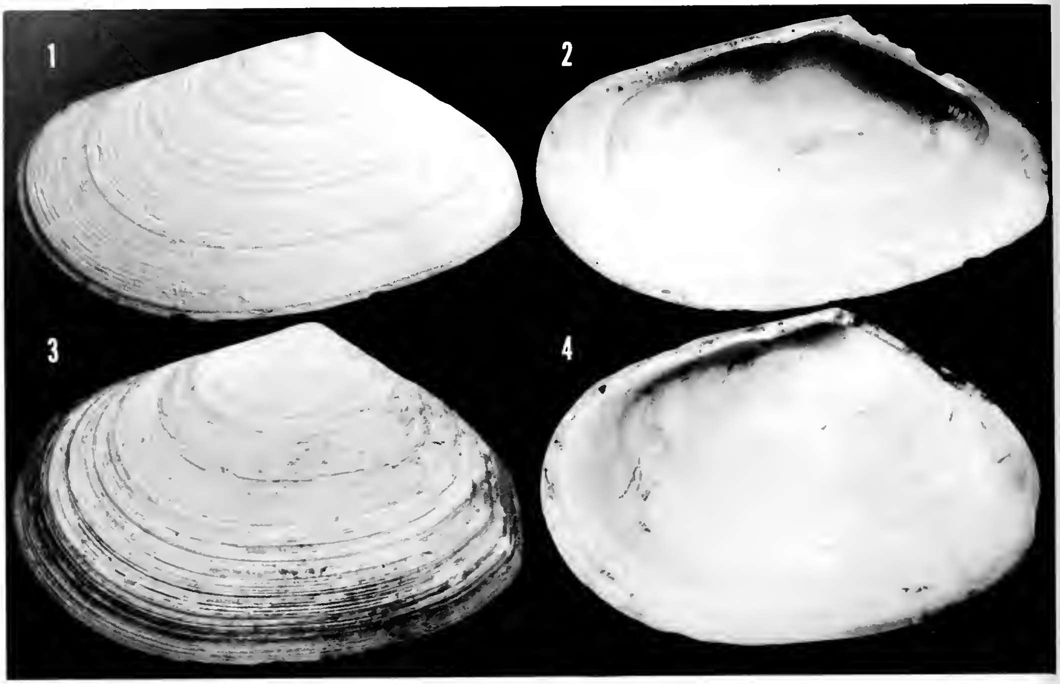

Plate 18. Figs. 1 and 2. Paratype of *Tellina (Maerella) gilchristi* Sowerby, off Cape Point, South Africa, SAM 14751 (length = 18.8 mm): Fig. 1, external view of the left valve; Fig. 2, internal view of the right valve. Figs. 3 and 4. *Tellina (Maerella) analogica* Sowerby, Baboon Point, Saldanha Bay, SAM 14996 (length = 18.3 mm): Fig. 3, external view of the left valve; Fig. 4, internal view of the right valve.

slightly raised, short nymphal callosities; escutcheon and lunule indistinct, obscure, elongate, and lanceolate. Hinge line moderately developed. In left valve, cardinal complex consisting of anterior, protuberant, narrowed bifid tooth with subequal lobes, and of posterior oblique, elongate, thin laminate tooth adpressed to base of nymphal callosity; no true lateral teeth, but hinge line slightly thickened anteriorly and posteriorly. In right valve, cardinal complex consisting of posterior, very narrow, bifid tooth with subequal lobes and of anterior somewhat thickened laminate tooth; posterior lateral tooth distal, shelf-like, pointed, with small socket above; anterior lateral tooth stronger, more proximal to cardinal complex, upcurled, pointed, socketed, with central flange contiguous with anterior laminate cardinal tooth.

Muscle scars moderately impressed. Anterior adductor muscle scar irregularly oval; posterior adductor muscle scar irregularly subquadrate. Pallial sinus equal in both valves, rising rather steeply posteriorly, rounded dorsally, gently descending in irregular convex arcuation, rounded anteriorly and recurving to unite with pallial line basally; confluence extensive, over three quarters of ventral length of pallial line; pallial sinus well separated from anterior adductor muscle scar. Cruciform muscle scars obscure, irregularly rounded, small, far posterior, and close to shell margin. White, shining, with rather chalky texture; some specimens with grayish dehiscent periostracum peripherally; marked subpellucid concentric bands.

Length mm	Height mm	Width mm	
22.1	14.6	06.5	Baboon Point, Saldanha Bay
21.5	14.0	05.5	holotype of *analogica*
18.7	11.9	05.2	off Bottel Fontein, Helena Bay
16.3	10.1	—	Baboon Point, Saldanha Bay

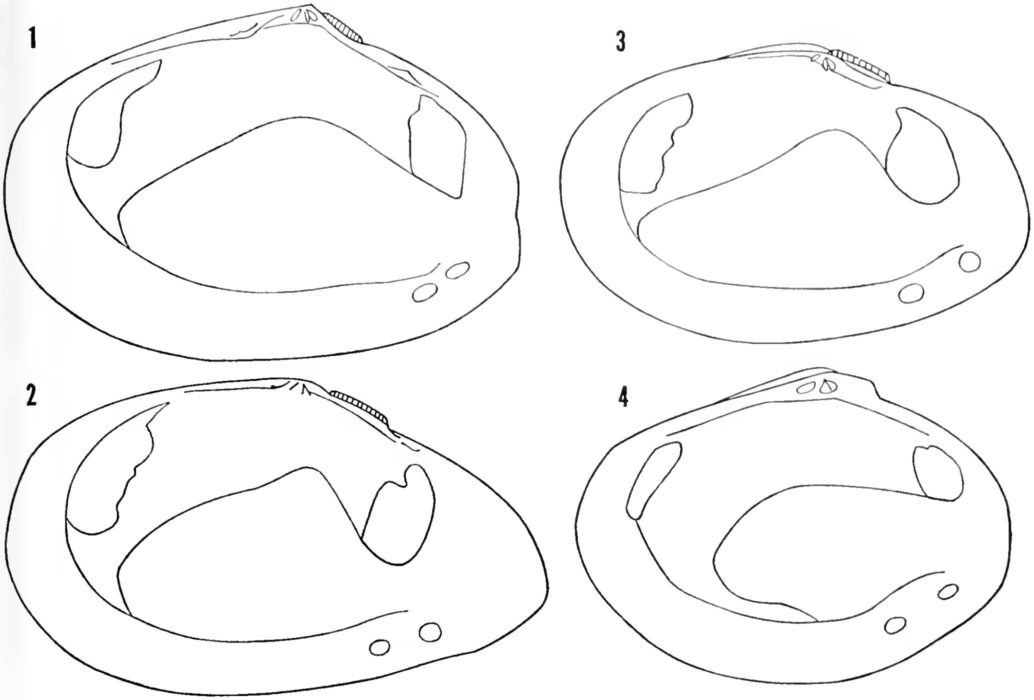

Plate 19. Diagrammatic illustrations of the internal surface of the valves, showing the dental configuration and muscle scars of the right valve. Fig. 1. *Tellina (Maerella) analogica* Sowerby, Baboon Point, Saldanha Bay, South Africa, SAM 14996 (length = 19.1 mm). Fig. 2. *Tellina (Fabulina) fabula* Gmelin, "Natal" [in error], SAM A30016 (length = 19.5 mm). Fig. 3. *Macoma (Scissulina) dispar* (Conrad), Goh Sindorar Nua, Thailand, USNM 661365 (length = 16.9 mm). Fig. 4. *Heteradonax ludwigii* (Krauss), Delagoa Bay, Mozambique, SAM A30021 (length = 15.8 mm).

Remarks. The whereabouts of the holotype of *Tellina analogica* Sowerby is unknown. Barnard (1964b) could not find the type, and it is not in the type collection of the British Museum (Natural History).

Since only a relatively few specimens are known, it appears that this species is quite rare. Both Sowerby (1904) and Barnard (1964b) have pointed out that *T. analogica* is closely allied to *T. gilchristi*, and Barnard even suggested that they might be indistinguishable and synonymous. The species are sympatric and very closely related; their hinge elements, especially the lateral teeth, and the configuration of their pallial scars are virtually the same. But the few specimens available seem quite distinct from *T. gilchristi*. Although the outline of the valves varies from subtrigonal to subrectangular, *T. analogica* is proportionately higher and wider that *gilchristi*. The posterior truncation of *analogica* is more blunt and usually biangulate, while in *gilchristi* the posterior end appears to be more distinctly pointed. Further, the shell of *analogica* is white, whereas *gilchristi* is normally rayed or banded with pink or red. White individuals of the latter have the usual longer dimensions, a narrowed posterior aspect, and are distinguishable from *analogica*.

Range. Tellina analogica is a southwest African species living in depths to 160 m in soft substrates from north of Lüderitz Bay to Saldanha Bay, Cape Province. Dell (1964) reported it from Tristan da Cunha in 40 m.

Specimens examined. REPUBLIC OF

SOUTH AFRICA: 26°32′S; 14°50′E, N of Lüderitz Bay in 160 m (UCT); 32°24′S; 18°07′E, NW of Bottel Fontein, Helena Bay in 69 m; 33°02′S; 17°58.9′E, Saldanha Bay, in 16 m (UCT); off Baboon Point, Saldanha Bay in 31 fms. (57 m) (SAM).

Subgenus *Angulus* Megerle von Mühlfeld

Angulus Megerle von Mühlfeld 1811, Gesellschaft Naturforschender Freunde Berlin, Magazin, 5: 57 (type-species, *Tellina lanceolata* Gmelin 1791, subsequent designation, Gray 1847, p. 186).

Oudardia Monterosato 1884, Nomenclatura generica e specifica di alcune Conchiglie Mediterranee, Palermo, p. 22 (type-species, *Tellina oudardii* Payraudeau 1826 [= *T. compressa* Brocchi 1814], original designation).

Moerella 'Fischer' Gardner 1928, U. S. Geol. Sur., Prof. Paper 142-E: 195, *non* Fischer 1887.

Anbulus Megerle von Mühlfeld. McLean 1951, New York Acad. Sci., Scientific Survey of Porto Rico and Virgin Islands, 17 (1): 96, error for *Angulus*.

Description. Shell small to medium in size, fragile to solid, ovate to elliptical in shape, with the left valve generally more convex and with a flexure to the right posteriorly. Sculpture primarily concentric and weakly incised over the surface of the valves; rarely differentiated along the posterior dorsal slope. Hinge without lateral dentition in the left valve. Right valve with the anterior lateral tooth adjacent to the cardinal complex and with an obsolete posterior lateral tubercle. Pallial sinus generally extensive, confluent with the pallial line for much of its ventral length.

Numerous interpretations of *Angulus* have been utilized—none perhaps as ambiguous and as broad as that of Megerle von Mühlfeld (1811). In designating a type-species, Gray (1847) diminished the original extent of *Angulus*. Salisbury (1934) went so far as to claim that only two species belonged to the group *sensu stricto* —the type-species *T. lanceolata* Gmelin, and another, probably synonymous, *T. armata* Sowerby. Yet Salisbury used *Angulus* at least five times in naming the species he figured. Some authors (Gardner, 1928; Olsson and Harbison, 1953) have used *Moerella* for species that had previously been placed in *Angulus*. Admittedly the interpretation of the dental configuration is most important, and *Moerella*, with *T. donacina* Linnaeus as type-species, has a strong right posterior lateral tooth. *Angulus*, then, is reserved for those species with that tooth weak, obsolete, or absent. Nevertheless, the system is still unsatisfactory, because the posterior lateral dentition is difficult, if not impossible, to quantify.

Tellina (Angulus) canonica Salisbury
Plate 14, figure 4; Plate 20, figures 1, 2.

Tellina regularis Smith 1904, Jour. Malacology, 11 (2): 25, 39, pl. 3, fig. 18 (type-locality, Port Alfred, Cape Colony; syntypes, BMNH 1903.12.-19.1281–95), *non* Carpenter 1855.

Tellina canonica Salisbury 1934, Proc. Malac. Soc. London, 21 (2): 86, new name for *T. regularis* Smith 1904, *non* Carpenter 1855.

Description. Shell extending to 14 mm in length and to 10 mm in height, subrectangular to suboval, inequilateral, equivalve, fragile to subsolid, compressed, with weak posterior flexure to right. Umbos behind middle, small, inconspicuous, pointed, opisthogyrous, and not inflated or elevated. Anterior margin broadly to narrowly rounded; ventral margin gently convex, rising slightly posteriorly; anterior dorsal margin long, gently descending, and usually straight; posterior dorsal margin short, steeply descending, and straight; posterior margin short, straight to weakly convex, and forming broad, blunt, oblique truncation. Sculpture consisting of concentric, closely spaced, incised lirations tending to become somewhat acentric peripherally and obsolete posteriorly in left valve, and of fine obsolete radial vermiculations. Posterior ridge absent, indistinct, or weak.

Ligament yellow-brown, protuberant, short, not well developed, set in weak, lanceolate escutcheon; lunule lanceolate, long, weak, and indistinct, but stronger in left valve; internal extension of ligament

present and subtending low, indistinct nymphal callosities. Hinge with rather fragile dentition. In left valve, cardinal complex consisting of anterior, weak, narrow bifid tooth with subequal lobes, and of posterior, thin, laminate tooth subtending oblique lateral internal ligament and often broken or lost; lateral teeth absent or obsolete, consisting of distal, weak thickenings of hinge line. In right valve, cardinal complex consisting of posterior, narrow, weak, elongate, bifid tooth with subequal lobes, and of anterior short, protuberant, somewhat thickened laminate tooth; anterior lateral tooth strong, shelf-like, protuberant, subproximal to cardinal complex, and weakly upturned; posterior lateral tooth distal, weak, laminate, and socketed above.

Muscle scars weakly impressed. Anterior adductor muscle scar flattened dorsally and rounded ventrally; posterior adductor muscle scar irregularly subrectangular. Pallial sinus more or less equal in both valves, rising only slightly posteriorly, weakly convex dorsally, irregularly descending, roundly pointed anteriorly, well separated from anterior adductor muscle scar and recurving basally to unite with pallial line for about three quarters of its ventral length. Cruciform muscle scars irregularly rounded, closely juxtaposed with right anterior subrectangular scar. Color white with central suffusions of yellow, pellucid, shining and polished internally.

Length mm	Height mm	Width mm	
14.5	10.1	—	Port Alfred, near Grahamstown
14.0	10.0	04.5	syntype of *regularis*
11.0	07.8	—	Still Bay
10.1	07.4	03.8	East London
07.1	05.2	02.5	East London

Remarks. Tellina canonica appears to be rather rare. Its most variable characteristic is the outline of the valves. Though it is usually somewhat subrectangular, with an oblique posterior truncation, short specimens tend to be oval, with a broadly arcuate anterior margin and a short convex ventral margin. Typically the shell is suffused centrally with yellow, but this coloration may be completely lacking, in which case the shell is simply a pellucid white.

The unique, minute internal ligament, which is a ventral oblique branch of the anterior portion of the larger external ligament, distinguishes *T. canonica* from other South African tellinids. This structure is quite similar to the configuration encountered in *T.* (*Cadella*) *semen* and can even be compared to the internal ligament of the semelid *Semelangulus*. A strong, distinct internal resilium, resting on a chondrophore, characterizes the family Semelidae. Both *T. canonica* and *T. semen* exhibit an incipient internal ligament and, in this respect, converge with each other as well as with the Semelidae.

Tellina canonica is included in *Angulus* since it has the anguloid facies of a poorly developed or obsolete right posterior lateral tooth and of a thin, shelf-like, right anterior lateral tooth closely juxtaposed to the cardinal complex. Along with a number of other closely related tellens—the *T. rutila* Dunker complex of the Indo-Pacific, *T. tenuis* da Costa in the eastern Atlantic, *T. tampaensis* Conrad, *T. mera* Say, and *T. paramera* Boss in the western Atlantic, and *T. suffusa* Dall and *T. meropsis* Dall of the eastern Pacific—*T. canonica* departs in its subrectangular-subovate, subtrigonal shape from the typically elongate-lanceolate anguloids, as seen in the type-species of *Angulus, T. lanceolata.*

Martin (1956; 1962) found this species in Pleistocene deposits at Sedgefield, west of Knysna.

Range. In South Africa, this species occurs from Still Bay to East London. Barnard (1964b) recorded it from Port Elizabeth and Jeffreys Bay. Boshoff (1965) found it among *Cymodocea* near Ilha des Portugueses, Inhaca, Mozambique. Evidently it prefers soft substrates like black mud, although it has been taken in sand (van Bruggen, 1962).

Specimens examined. REPUBLIC OF SOUTH AFRICA: False Bay in 18 m (UCT); Still Bay (SAM); Sedgefield (SAM); Port Alfred (BMNH; MCZ; SAM; USNM); East London (NM).

Species Incorrectly Placed in the Tellininae

At least two well-known tellinacean bivalves in South Africa have been treated frequently and incorrectly in the genus *Tellina.* They are discussed in the following section.

Macoma (*Scissulina*) *dispar* (Conrad)
Plate 19, figure 3; Plate 20, figure 3.

Tellina dispar Conrad 1837, Jour. Acad. Nat. Sci. Philadelphia, 7: 259 (type-locality, inhabits the Sandwich Islands [Hawaiian Islands]; type, not found in ANSP; not listed in Moore, 1962).

Tellina fabula var. *major* Krauss 1848, Die südafrikanischen Mollusken, p. 3 (type-locality, in der Natalbai; types, ? Stuttgart).[1]

Tellina (*Fabulina*) *dispar* Conrad. Bertin 1878, Nouv. Arch. Mus. Natl. Hist. Nat. Paris, 1: 277, no. 117.

Tellina (*Scissulina*) *dispar* Conrad. Dall 1924, Proc. Biol. Soc. Washington, 37: 88.

Tellina fabula 'Gmelin' Turton 1932, The marine shells of Port Alfred, South Africa, p. 248, pl. 67, no. 1751, *non* Gmelin 1791.

Description. Shell extending to 33 mm in length and to 23 mm in height, elongate to subrectangular, slightly inequilateral, inequivalve, subsolid, slightly inflated, with left valve of greater convexity than right and with definitive posterior flexure to right. Umbos slightly behind middle, rounded, not elevated, blunt, and slightly inflated. Anterior margin broadly and smoothly rounded; ventral margin gently convex rising in arcuation posteriorly; anterior dorsal margin long, gently descending and gently convex; posterior dorsal margin shorter, more steeply inclined, more or less straight, occasionally concave; posterior margin short, straight to weakly convex, forming blunt, oblique truncation. Sculpture consisting of more or less regular, weakly developed concentric striations, strongest on anterior and posterior slope of right valve; growth lines sometimes evident; scissulate or acentric sculpture on right valve only and consisting of finely incised, closely set sulcations crossing concentric lirations over central disc of valve; weak radial vermiculations evident on left valve but no scissulations on left valve; weak, gently posterior ridge in right valve.

Ligament light brown to black, rather strong, protuberant, set on flattened and slightly raised nymphal callosities; escutcheon obsolete or absent; weak, indefinite lunule. Hinge line weakly developed. No lateral teeth. Left cardinal complex with anterior, narrow, bifid tooth and posterior elongate, thin, laminate tooth closely adpressed to base of nymphal callosity; sometimes obsolete or lost. Right cardinal complex with posterior, narrow, often skewed, bifid tooth, and anterior, protuberant, thickened, subdeltoid tooth. Internal, somewhat thickened, anterior rib present in both valves.

Muscle scars moderately well impressed. Anterior adductor muscle scar irregularly elongate and curved; posterior adductor muscle scar irregularly rounded to subquadrate. Pallial sinus more or less equal in opposite valves, rising rather abruptly posteriorly, arched dorsally beneath the beaks, descending gently to unite with pallial line in gentle arcuation anteriorly. Pallial sinus extending very close to base of anterior adductor muscle scar, usually slightly separated from it, infrequently becoming subcoalescent. Cruciform muscle scars difficult to discern, rather closely set, rounded or sometimes slightly flattened, close to margin of shell. Color basically white, frequently with central and umbonal suffusions of yellow, rarely pinkish or pale orange suffusions umbonally; translucent

[1] It cannot be certain that Krauss's specimens from Natal Bay were *M. dispar*, since he says, "Ich habe Exemplare aus europäischen Meeren verglichen und kann zwischen diesen und den meinigen in Form und Zeichnung nich den geringsten Unterschied finden, nur in der Grösse übertreffen sie die europäischen ums Doppelte."

Plate 20. Figs. 1 and 2. *Tellina* (*Angulus*) *cananica* Salisbury, East London, South Africa, NM 2983 (length = 10.2 mm): Fig. 1, external view of the left valve; Fig. 2, internal view of the right valve. Fig. 3. *Macoma* (*Scissulina*) *dispar* (Conrad): external view of the right valve, to show fine acentric sculpture, Santa Carolina, Bazaruta Bay, Mozambique, MCZ (length = 26.2 mm). Fig. 4. *Heteradonax ludwigii* (Krauss): external view of the right valve, Delagoa Bay, Mozambique, SAM A30021 (length = 23 mm).

in young stages; generally shining or polished internally.

Length mm	Height mm	Width mm	
32.8	22.5	10.3	Hilo, Hawaii
31.7	23.0	09.7	Hawaiian Islands
26.3	17.1	07.4	Durban
24.9	16.8	06.8	Durban Bluff
22.3	14.5	06.2	Cocos-Keeling Id.
14.2	08.6	03.7	Mala Bay, Maui, Hawaii

Remarks. The nature of the dentition is of subfamilial importance in the Tellinidae. The Macominae are laterally edentate, whereas the Tellininae have one to four variously developed lateral teeth. Notwithstanding the obsolescence or disappearance of certain lateral dental elements in the Tellininae, all Tellininae have some development of the right anterior lateral tooth, even though that tooth may be almost incorporated into the cardinal complex, as in *T.* (*Homalina*) *trilatera* (*q.v.*).

The complete absence of lateral dentition in *S. dispar*, and particularly the lack of any evidence of a right anterior lateral tooth, indicates that this species is not a *Tellina* and, further, that it is truly of macomoid affinities. The species has been variously dealt with in the literature and has been considered in the superspecific grouping named *Fabulina* Gray 1851 with *Tellina fabula* Gmelin as type-species. As a matter of fact, *S. dispar* has been con-

fused with *T. fabula* which is of European distribution (Forbes and Hanley, 1848; Grossu, 1962). Barnard's remark (1964b: 545) is illustrative: "The identification of Natal shells with an Indo-Pacific species is preferable to identifying them with a European species (*fabula*). No European material is available for comparison." Unfortunately, there was European material available to Barnard, but these specimens were labelled as coming from Natal (SAM A 30016). This lot consists of a good series of specimens of *T. fabula* that somehow were brought from Europe and found their way into the collection with incorrect locality data. There is no indication that *T. fabula* lives or ever lived in South African or Indo-Pacific waters.

T. fabula and *S. dispar* are easily distinguished (see Pl. 19, figs. 2 and 3); the former has a right anterior lateral tooth, whereas the latter, as mentioned above, does not. In addition to this fudamental difference, the shells of each species are of different shapes, that of *fabula* being rather pointed or attenuate behind, that of *dispar* rather bluntly truncate. Their similarity consists in being acentrically sculptured on the right valve only, and is the result of convergence (Boss, 1966a). This unique type of sculpture is widespread within the Tellinacea and particularly within the Tellinidae. Both the Tellininae and the Macominae have a number of species that are scissulate. The very closely related macomoids, *Jactellina* Iredale 1929 and *Loxoglypta* Dall, Bartsch, and Rehder 1938, exhibit scissulate sculpture on both right and left valves. Occasionally, *Loxoglypta rhomboides* (Quoy and Gaimard) has been taken in East Africa, including the warm waters of Natal.

Macoma (*Scissulina*) *dispar* lives in relatively shallow water from below the low tide zone to depths of up to 10 fathoms. Most often it is encountered in calcareous sandy bottoms with a relatively coarse texture. Maes (1967) found it commonly in the lagoons at Cocos-Keeling.

Range. Macoma (*Scissulina*) *dispar* is found throughout the central Indo-Pacific area, from the coast of southeast Africa to as far east as the Society Islands and the Hawaiian Islands. Although Turton (1932) recorded this species from Port Alfred, the southernmost area in which the species has been collected alive in South Africa is in the vicinity of Durban.

Specimens examined. REPUBLIC OF SOUTH AFRICA: (BMNH); Durban (SAM; NM); Durban Bluff (NM). MOZAMBIQUE: Santa Carolina Id., Bazaruto Bay (MCZ). MADAGASCAR: Nosy Satrana; Ilampy and near Ankobahahoba, NE of Ambodifototra, Ile Ste. Marie (all MCZ). SEYCHELLES IDS.: (MCZ; USNM). MAURITIUS: (BMNH). MALDIVE IDS.: (BMNH); NW of Gadifurils, South Nilandu Atoll; off Imma Id., SE side North Male Atoll (both ANSP). COCOS-KEELING IDS.: W of Pulo Bras and Pulo Gangsa, SW end of Direction Id., N. Lagoon, West Id., and off Home Id. (all ANSP). THAILAND: Goh Sindarar Nua (USNM). INDONESIA: E of Mios Woendi, Madaido Ids., New Guinea (MCZ). PHILIPPINE IDS.: Calapan, Mindoro (MCZ); S of Bohol (BMNH). AUSTRALIA: Percy Ids. (BMNH) and Heron Id. (MCZ), Queensland. PALAU IDS.: Schonian Harbor, N of Peleu Id. (ANSP). CAROLINE IDS.: (ANSP). MARSHALL IDS.: Kwajelein Atoll (MCZ). GILBERT IDS.: Apiang, Kingsmill Ids. (MCZ). LOYALTY IDS.: Mare (MCZ). NEW CALEDONIA: (MCZ). FIJI IDS.: Viti Levu (ANSP). SAMOA IDS.: off Manono Id., Upolu Id., and off Amouli, Tutuila Id. (both MCZ). COOK IDS.: Akitua, NW of Maina Id., near Nikaupara Village, S of Rapota Id., all Aitutaki (all ANSP). SOCIETY IDS.: Tahiti (MCZ); N of Motuorini Point, Tahiti (ANSP). LINE IDS.: Palmyra (MCZ). HAWAIIAN IDS.: Hilo, Hawaii (ANSP; MCZ; USNM); Mala Bay, Maui; Kawaikapu, Molokai; Ford's Id., Pearl Harbor; Honolulu (all USNM); Waikiki Beach (ANSP); Kahana

Bay (ANSP; MCZ); Mokuloelue Id. and Coconut Id., Kaneohe Bay (both ANSP); near Heeia Pond (fossil); Kaaawa (both USNM); Aiea; Kauai (both ANSP).

Heterodonax ludwigii (Krauss)
Plate 19, figure 4; Plate 20, figure 4; Plate 21.

Tellina ludwigii Krauss 1848, Die südafrikanischen Mollusken, p. 3, pl. 1, fig. 2 (type-locality, In litore natalensi; holotype, ? Stuttgart).

Tellina ludwigi Krauss. Sowerby 1892, Marine shells of South Africa, p. 57, error for *ludwigii* Krauss.

Tellina queketti Sowerby 1897, Appendix to Marine shells of South Africa, p. 22, pl. 8, fig. 16 (type-locality, Durban; types, not in BMNH type-collection).

Tellina queketti var. *radiata* Sowerby 1897, Appendix to Marine shells of South Africa, p. 22, pl. 8, fig. 17 (type-locality, Durban; types, not in BMNH type-collection), *non* Linnaeus 1758.

Tellina queeketti Sowerby. Schwarz 1910, Trans. Geol. Soc. South Africa, 12: 115, error for *queketti* Sowerby.

Description. Shell extending to 23 mm in length and 17 mm in height, irregularly subrectangular to subelliptical, equilateral to slightly inequilateral, equivalve, rather solid, inflated, with valves of more or less equal convexity, and without posterior flexure. Umbos subcentral, somewhat behind middle, slightly elevated, inflated, and blunt. Anterior margin smoothly and narrowly rounded; ventral margin convex, rising posteriorly, sometimes bowed midventrally; anterior dorsal margin long, more or less straight, and gently descending; posterior dorsal margin short, more or less straight, and more steeply descending; posterior margin weakly convex and forming blunt oblique truncation. Sculpture consisting of extremely weak and fine striations; irregular round growth lines evident; no radial sculpture developed.

Ligament black-brown, protuberant, set upon raised nymphal callosities; no true escutcheon; lunule weakly developed, elongate, lanceolate, striate. Hinge line moderately developed. In left valve, cardinal complex consisting of single, thickened, irregularly subdeltoid, bifid tooth (posterior cardinal element usually not evident); no lateral teeth. In right valve, cardinal complex consisting of posterior, irregularly subdeltoid, thickened, bifid tooth, and of anterior strong, thickened tooth; no true lateral teeth, but often hinge margin anteriorly and posteriorly socketed distally, forming weak, shelf-like, elongate grooves.

Muscle scars variously impressed; adductors set relatively high in valves; anterior semilunate, posterior irregularly rounded to subquadrate. Pallial sinus equal in opposite valves, extending straight out from base of posterior adductor muscle scar, rounded anteriorly, irregularly and arcuately falling to pallial line; confluence short. Cruciform muscle scars large, rounded, and not easily discerned. Color, white, purple, cream or pinkish, frequently with irregular radial rays of purple or violet evident externally and internally.

Length mm	Height mm	Width mm	
22.8	16.8	09.6	Delagoa Bay
21.6	16.2	08.3	Isipingo, Natal
19.4	15.6	08.7	Durban
17.6	12.7	06.3	Durban
15.8	11.5	06.2	Delagoa Bay
06.1	04.6	01.9	Morrumbene Estuary

Remarks. This species has long been incorrectly considered a *Tellina* (see Barnard, 1964b: 542, for citations). However, both its shell morphology (Pl. 19, fig. 4) and its anatomy (Pl. 21) indicate that it has affinities with other Tellinacean bivalves. It is separated from the genus *Tellina* and, indeed, the family Tellinidae, by (1) the development of distinctly raised nymphal callosities and the breadth of the hinge plate; (2) the presence of an unusual coloration, particularly the violaceous suffusions and radial rays; (3) the obsolescence and loss of the left posterior cardinal tooth and the generalized stoutness of the remaining cardinal teeth; (4) the lack of definitive lateral teeth; (5) the lack of a developed escutcheon; (6) the presence of plicate gills; and (7) the smallness of the palps. The composite features of this

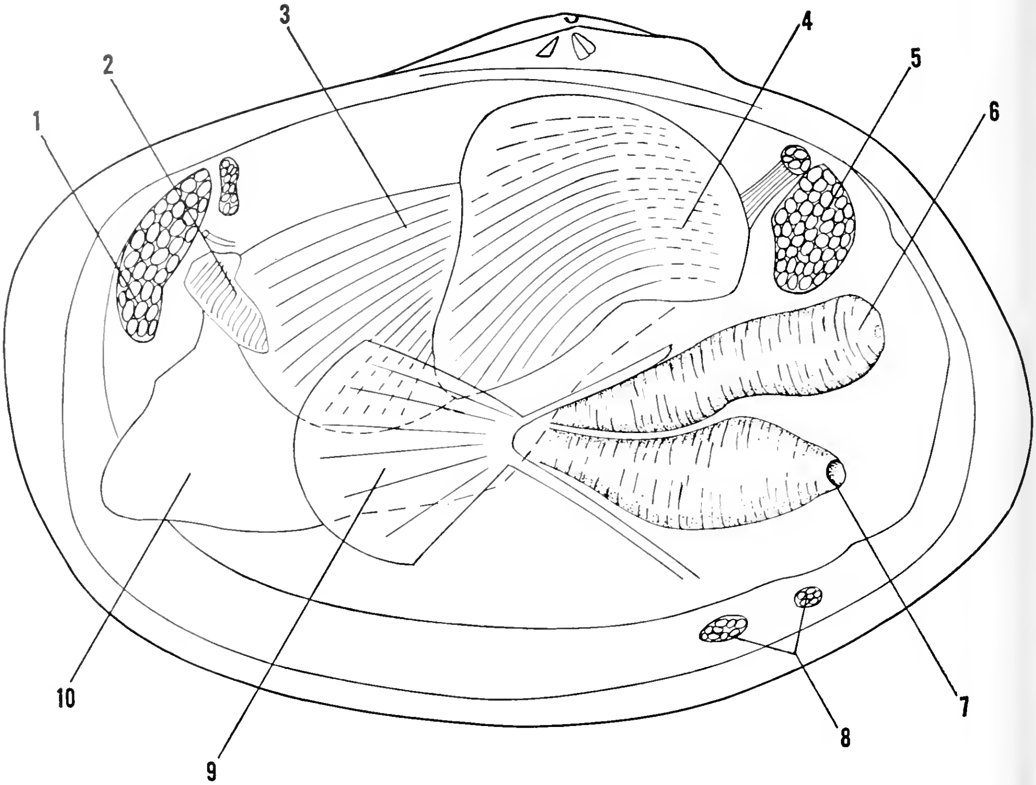

Plate 21. Diagrammatic illustration of the anatomy of *Heterodonax ludwigii* (Krauss): 1, anterior adductor muscle; 2, labial palp; 3, inner demibranch; 4, outer demibranch; 5, posterior adductor muscle; 6, excurrent siphon; 7, incurrent siphon; 8, cruciform muscle; 9, siphonal retractor muscles; 10, foot.

species agree in detail with the diagnosis of the genus *Heterodonax* Mörch 1853 (type-species, by monotypy, *Tellina bimaculata* Linnaeus 1758) as given by Dall (1900: 973), Thiele (1935: 908) and Olsson (1961: 354).

The genus *Heterodonax* belongs to the family Psammobiidae. Anatomically, it is characterized by plicate gills and small palps. The ligament is set upon a raised nymph, and the hinge plate is broad. There are really no lateral teeth present, and an escutcheon is not developed. The general features of the Psammobiidae, namely the nature of the gills and palps, are illustrated in *Gari tellinella* (Yonge 1949: 37, fig. 6). Further, the purple shell coloration, with its tendency to ray formation, is often encountered in the Psammobiidae and particularly in *Heterodonax*. For these reasons the species named *Tellina ludwigii* by Krauss is here removed from *Tellina* and placed in *Heterodonax*.

Heterodonax ludwigii exhibits a considerable amount of variation, especially in regard to shape and coloration. Further, the outline of the valves changes during ontogeny. In smaller, immature specimens there is a tendency to be proportionately more elongate or rather subelliptical in outline, whereas in adults the shell is somewhat more rounded to subrectangular. Some individuals may have a tendency to pointedness posteriorly, and frequently the

ventral margin is bowed out in an irregular convexity, giving the outline of the valves a ventral bulge.

Basically the shell is white, but not infrequently specimens may be predominantly purple, cream, or pink. Rayless white specimens do occur, but more often individuals rayed in purple are encountered. The rays are irregular in number, may be interrupted by concentric white bands, and usually widen peripherally.

The fossil history of *H. ludwigii* has been reviewed by Barnard (1962b: 194), who documented the occurrence of the species from the Algoa Bay area, in the Pleistocene, from the following localities: Shark River, The Creek (Ferreira's River), Zwartkops River, Redhouse, Koege River, Coerney, and Bushman's River.

This species appears to inhabit relatively shallow water in sandy substrates. As recorded by Broekhuysen and Taylor (1959: 292), it was taken in a sand bar in the estuary at Kosi Bay, where the pH was decidedly alkaline (8.5–8.7) and there was a considerable range in salinity (21.2–32.9 ppt). Specimens have also been taken in the Morrumbene Estuary. Therefore, this species is not unlike some of the donacids and certain psammobiids in having a preference for estuarine conditions, probably because of the considerable amounts of suspended matter released into the environment by the outflow of the rivers.

Contrary to Barnard (1964b: 543), the specimen named by Tomlin (1926: 301) as *Tellina yemenensis* Melvill is preserved in the Natal Museum (no. 3987) and is not *H. ludwigii;* it is treated in the previous section of this paper separately.

A species closely related to *H. ludwigii* is *H. seychellarum* Bertin (Bertin, 1881: 118, pl. 3, fig. 6a, b). However, this species from the Seychelles is differently shaped, being more nearly rounded and without the ventral bulge often found in *H. lugwigii.* Further, it appears to be completely purple and less frequently, if ever, rayed.

Range. H. ludwigii is found along the east coast of Africa, from at least northern Mozambique to Durban. In the Pleistocene it lived as far south as Algoa Bay but does not live there presently, a situation noted by Schwarz (1910).

Specimens examined. REPUBLIC OF SOUTH AFRICA: Durban (SAM; NM); Durban Bluff (DM; NM); Isipingo, Natal (NM). MOZAMBIQUE: Delagoa Bay (SAM); Kosi Bay; Morrumbene Estuary, near Inhambane (both UCT).

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The Spider Subfamily Castianeirinae of North and Central America (Araneae, Clubionidae)

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Castianeira longipalpus, male. Pedipalps lost during the final moult. (Photo by H. K. Wallace.)

Castianeira cingulata, male. (Photo by H. K. Wallace.)

Castianeira crocata, female. The longitudinal abdominal stripe is bright orange-red. (Photo by H. K. Wallace.)

THE SPIDER SUBFAMILY CASTIANEIRINAE OF NORTH AND CENTRAL AMERICA (ARANEAE, CLUBIONIDAE)[1]

JONATHAN REISKIND[2]

CONTENTS

ABSTRACT

A new subfamily, the Castianeirinae, is proposed for most of the clubionid members of the Micariinae (a gnaphosid subfamily). This revision includes the four genera (*Castianeira*, *Mazax*, *Myrmecotypus*, and *Sphecotypus*), with 59 species, that represent this subfamily in North and Central America.

Seventeen species are newly described: *Castianeira thalia*, *C. occidens*, *C. alfa*, *C. athena*, *C. rothi*, *C. azteca*, *C. zembla*, *C. rica*, *C. alba*, *C. guapa*, *C. abuelita*, *C. trimac*, *Mazax xerxes*, *M. chickeringi*, *M. ajax*, *Myrmecotypus olympus*, and *M. orpheus*. One new name is proposed, *Mazax pax*, and 16 new synonymies recognized.

The evolution of the group, with special emphasis on the impact of selection for ant mimicry, is discussed.

INTRODUCTION

The Castianeirinae, newly proposed in this revision, is a subfamily of the Clubionidae. It represents a major portion of the old Micariinae of Simon (1897). Although no comprehensive revision of this group has ever been published, three works include a good number of the species: O. P.-Cambridge (1889–1902), F. P.-Cambridge (1897–1905), and Chickering (1937).

The group is world-wide, though predominantly tropical. This revision includes the fauna of North and Central America. The Central American fauna represents merely the small part of a vast array of species in the tropics of South America. Many members of the Castianeirinae exhibit ant mimicry, a phenomenon that has greatly influenced the past and present classification of the group.

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[1] This study is part of one presented to the Department of Biology at Harvard University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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RECLASSIFICATION OF THE MICARIINAE

The Micariinae as recognized by Roewer (1954) and Bonnet (1961) is a subfamily of the Clubionidae. The predominantly holarctic ant-mimicking genus, *Micaria*, is the type-genus of the subfamily. Table 1 includes the 39 genera in the subfamily with their 368 species. This subfamily is not only polyphyletic but includes representatives of at least three other spider families and two clubionid subfamilies.

First, the type-genus, *Micaria*, should be placed in the family Gnaphosidae and not in the Clubionidae. Locket and Millidge (1951) point out the intermediate position of the genus between the Clubionidae and Gnaphosidae and also conclude that it should be placed in the Gnaphosidae. The following reasons account for this placement:

(1) The anterior spinerets are cylindrical, moderately sclerotized, and fairly widely separated. Locket and Millidge (1951) observe that they "are not separated noticeably as in the Gnaphosidae," but neither are they the conical, unsclerotized, adjacent anterior spinerets typical of the Clubionidae. In balance they are more gnaphosid than clubionid.

(2) The genital structures are more like those of the Gnaphosidae than the Clubionidae. Jackson (1932) states, "I believe these Micariae should be assigned to the family Gnaphosidae with which they entirely agree in the structure of their sexual organs. Their resemblance to the genus *Phrurolithus* of the Clubionidae is due to convergence. . . ." Both the male pedipalps and female epigyna are basically gnaphosid, the genital bulb of the male often oval with the embolus arising from its center, as in species of *Gnaphosa*, *Drassodes*, and *Geodrassus*, and the epigyna exhibiting a complexity found in the gnaphosids but not in the clubionids.

(3) The posterior median eyes are oblong (as is common in the Gnaphosidae) and not circular (as in all Clubionidae) (Locket and Millidge, 1951).

(4) Homann (1950) found the internal structure of the eyes of *Micaria* to resemble that of the Gnaphosidae (*Zelotes*) and to differ from that of the majority of recognized clubionid genera studied.

(5) "The leg scopulae consist of little spines which though widely spaced, are definitely spatulate; in Clubionidae of this size (e.g., *Phrurolithus*) the scopula hairs are aculeate" (Locket and Millidge, 1951).

Therefore *Micaria* and its closely related genus *Micariolepis* (a total of 108 species) must be tranferred to the Gnaphosidae, taking the name of their subfamily, the Macariinae, with them.

Five of the remaining 37 genera (representing 13 species)—*Chemmis*, *Anachemmis*, *Heterochemmis*, *Parachemmis*, and *Drassylochemmis*—are apparently Liocraninae. They have from four to six pairs of long spines on the tibia of the first pair of legs; the hairs on the abdomen are all simple; the epigyna and male pedipalps are similar to the liocranine genus *Agroeca*; and the labium, sternum, and endites are characteristically like those found in the Liocraninae. When describing *Drassylochemmis*, Gertsch and Davis (1936) placed the new genus in the Liocraninae and remarked on its close resemblance to *Anachemmis*.

Fifteen of the genera in Table 1 (accounting for 206 of the remaining 247 species) clearly constitute a monophyletic taxon within the Clubionidae. This taxon is of subfamilial rank. The largest genus of the old Micariinae is also the largest genus in this group—*Castianeira*, with 118 species. For this reason, and also because the only family-group name in the group, Myrmecidae Koch, 1851, is also used as a family-group name in the Formicidae (the Myrmeciinae), the name of this subfamily should be Castianeirinae. The new sub-

Table 1. Genera in the Micarinae According to Roewer (1954), with New Classifications

Genus (Type-species)	Author	Geographical Distribution	Number of Species	New Classification
Ceryerda (*C. cursitans*)	Simon, 1909	Australian	1	Molycriinae[1]
Honunius (*H. quadricauda*)	Simon, 1908	Australian	1	Molycriinae[1]
Jacaena (*J. distincta*)	Thorell, 1897	Oriental	1	Molycriinae[1]
Molycria (*M. mammosa*)	Simon, 1887	Australian	4	Molycriinae[1]
Myandra (*M. cambridgei*)	Simon, 1887	Australian	2	Molycriinae[1]
Sphingius (*S. thecatus*)	Thorell, 1890	Oriental	12	Corinninae?
Pesceennina (*P. epularis*)	Simon, 1903	Neotropical	1	?
Achalaicola (*A. vestita*)	Mello-Leitão, 1943	Neotropical	1	Prodidomidae
Aetius (*A. decollatus*)	O. P.-Cambridge, 1896	Oriental	1	Castianeirinae
Anachemmis (*A. sober*)	Chamberlain, 1920	Nearctic	3	Liocraninae
Anatea (*A. formicaria*)	Berland, 1927	Australian	1	Theridiidae
Apochinomma (*A. formicaeforme*)	Pavesi, 1881	Ethiopian Oriental Neotropical	2 3 8	Castianeirinae
Cambalida (*C. insulana*)	Simon, 1910	Ethiopian	3	?
Castanilla (*C. quinquemaculata*)	Caporiacco, 1936	Palaearctic	2	Castianeirinae
Castianeira (*C. rubicunda*)	Keyserling, 1879	Palaearctic Ethiopian Oriental Neotropical Nearctic	6 21 7 59 25	Castianeirinae
Chemmis (*C. frederici*)	Simon, 1898	Neotropical Nearctic	4 1	Liocraninae
Coenoptychus (*C. pulcher*)	Simon, 1885	Oriental	1	Castianeirinae
Copa (*C. flavoplumosa*)	Simon, 1885	Ethiopian Oriental	8 2	Castianeirinae
Corinnomma (*C. severum*)	Karsch, 1880	Ethiopian Oriental Australian Neotropical	1 8 2 1	Castianeirinae
Donuea (*D. decorsei*)	Strand, 1932	Ethiopian	1	?
Drassyllochemmis (*D. captiosus*)	Gertsch and Davis, 1936	Nearctic	1	Liocraninae
Graptartia (*G. granulosa*)	Simon, 1896	Palaearctic Ethiopian	1 1	Castianeirinae

[1] Lehtinen (1967) places the Molycriinae (= Myandrinae) in the Prodidomidae. Also see footnote p. 166.

TABLE 1. (*Continued*)

Genus (Type-species)	Author	Geographical Distribution	Number of Species	New Classification
Heterochemmis (*H. mirabilis*)	F. P.-Cambridge, 1899	Neotropical	2	Liocraninae
Liparochrysis (*L. resplendens*)	Simon, 1909	Australian	1	?
Mazax (*M. pax*)	O. P.-Cambridge, 1898	Neotropical	5	Castianeirinae
Merenius (*M. plumosus*)	Simon, 1909	Ethiopian	10	Castianeirinae
Messapus (*M. martini*)	Simon, 1898	Ethiopian	2	?
Methesis (*M. semirufa*)	Simon, 1896	Australian Neotropical	1 1	Corinninae ?
Micaria (*M. fulgens*)	Westring, 1851	Palaearctic Ethiopian Oriental Australian Neotropical Nearctic	59 2 1 2 4 37	Gnaphosidae Micariinae
Micariolepis (*M. dives*)	Simon, 1897	Palaearctic Ethiopian	2 1	Gnaphosidae Micariinae
Montebello (*M. tenuis*)	Hogg, 1914	Nearctic	1	?
Myrmecium (*M. rufum*)	Latreille, 1824	Neotropical	16	Castianeirinae
Myrmecotypus (*M. fuliginosus*)	O. P.-Cambridge, 1894	Neotropical Nearctic	7 1	Castianeirinae
Myrmeques (*M. attarum*)	Roewer, 1935	Neotropical	1	?
Parachemmis (*P. fuscus*)	Chickering, 1937	Neotropical	2	Liocraninae
Poecilipta (*P. janthina*)	Simon, 1896	Australian	2	Castianeirinae
Psellocoptus (*P. flavostriatus*)	Simon, 1896	Neotropical	1	Castianeirinae
Sphecotypus (*S. niger*)	O. P.-Cambridge, 1895	Oriental Neotropical	2 1	Castianeirinae
Supunna (*S. insularis*)	Simon, 1896	Australian	8	?

family is established and defined in the taxonomic section of this paper.[1]

Five genera (with 9 species) have previously been grouped in the subfamily Molycriinae (the Molycrieae of Roewer, 1954) and probably should again be considered a separate subfamily.

The type-species of *Methesis* (from Bolivia) is probably in the Corinninae, but the Australian member of the genus is clearly in the Castianeirinae. *Sphingius* is also probably in the Corinninae.

Two monotypic genera belong in other

[1] In his illuminating reclassification of the Araneomorpha, Lehtinen (1967) considers the Clubionidae to be a highly polyphyletic family. He places the Micariinae in the Gnaphosidae and raises the Corinninae and Liocraninae to familial status. Within this framework the Castianeirinae should be considered a subfamily of the Corinnidae.

distinct families. *Anatea* Berland has recently been redescribed and discovered to be in the family Theridiidae (Reiskind and Levi, 1967). Berland (1927) based his placement on the general antlike shape and the simple male genitalia (which superficially resembles that of *Micaria*). *Achalaicola* Mello-Leitão is in the Prodidomidae, a rare family related to the Clubionidae and Gnaphosidae.

The remaining eight genera, five of which are monotypic, may be members of the Castianeirinae, gnaphosids in the Micariinae, or members of entirely different taxa. Only careful examination and study will place them.

ANT MIMICRY AND ITS EFFECTS ON CLASSIFICATION

Ant mimicry is fairly common among spiders (Brignoli, 1966) and is most dramatic and widespread among the salticids and clubionids. The mimicry is basically Batesian: the innocuous mimic (spider) is protected by its resemblance to a noxious model (ant or velvet ant) by being mistaken for the model by potential predators.

Two results of selection for mimicry—convergence and extreme specialization—have produced errors in classification.

The convergence of superficial antlike characteristics in the mimics of several families of spiders led Walckenaer (1841) to create the genus *Myrmecia,* in which he included both clubionid and salticid ant mimics. Berland (1927) described an ant-mimicking spider, *Anatea formicaria,* and placed it among the ant mimics of the Clubionidae, although it is actually a theridiid (Reiskind and Levi, 1967). O. P.-Cambridge (1870) included *Aphantochilus,* an ant mimic related to the Thomisidae, in a group of clubionid ant mimics. Table 1 reviews the polyphyletic old Micariinae, which contained ant-mimicking clubionids (the new subfamily Castianeirinae) and gnaphosids (the new Micariinae).

Two families, which include only spiders that imitate ants, have been proposed. Koch (1851) established the family Myrmecidae, which included mostly clubionid ant mimics, with *Myrmecium* as the type-genus. The Aphantochilidae of Thorell, 1873, are thomisidlike spiders all mimicking cephalotine ants; the family includes four genera, with a total of eight species.

Specialization has also led to many ant-mimicking genera (e.g., *Myrmecium* and *Sphecotypus* in the Castianeirinae) that are satellites of a more generalized genus (e.g., *Castianeira* in the Castianeirinae) and earn their generic position by their bizarre and superficial mimetic characters.

Equal weighting of characters in the taxonomic analysis of a group that includes ant mimics would probably result in as absurd a classification as some of the foregoing examples. The external morphology is so extensively modified in ant mimics that carefully chosen characters, as little affected by selection for mimicry as possible, must be used in their proper classification.

PHYLOGENETIC RELATIONSHIPS OF THE GENERA

In attempting to trace the evolutionary history of a taxon, two basic approaches are used simultaneously—determination of (1) the real, homologous similarities between the taxon and its relatives, i.e., the phylogenetic relationships, and (2) the changes and differences resulting from evolutionary adaptations within the taxon itself. In both cases natural selection expresses itself in varying evolutionary rates for different characters.

Each character (or pleiotropic complex of characters) has its own evolutionary rate dependent upon the positive or negative selection on the character. This results in a taxon some of whose characters are "advanced" (i.e., the result of a high evolutionary rate and therefore new and different) while other characters are "primitive" (i.e., the result of a low evolutionary

rate and therefore similar to the characters of the ancestral taxa). When speaking of an "advanced" or "primitive" taxon, it is necessary to state clearly the characters being used. Sometimes a taxon is truly primitive, combining a vast group of primitive characters, e.g., the Liphistiidae, but usually it is a mixture of primitive and advanced characters; the taxon's "primitiveness" is a result of the subjective weighting of certain characters by the investigator. Characters of the same level of "primitiveness" usually do not group themselves, and for this reason the evolutionary history of a taxon must first be considered character by character. Only after such an analysis can speculation on the history of the taxon, as the total of all of its characters, take place.

Such an analysis of several important characters studied in the North and Central American Castianeirinae follows. These characters are (1) male genitalia, (2) female genitalia, (3) eye arrangements, (4) cheliceral teeth, (5) thoracic groove, and (6) mimetic characters.

Male genital structure. The tarsus of the male spider is modified as a copulatory organ for the transfer of sperm to the epigynum of the female. This structure is relatively distinct from species to species.

The male genital structure in the Castianeirinae is relatively simple compared to that in most spiders. As noted in the definition of the Castianeirinae, there is a basic pattern of homologous structures in all the male genitalia—the major piece of evidence that the whole subfamily is definitely a monophyletic taxon. The characteristics of the genitalia held in common include a tibia either with a small apophysis or lacking one entirely; a full, lateral, protective cymbium; and a genital bulb that has a globose base, is more or less elongated distally, and has a winding, highly sclerotized palpal duct that terminates at its distal end in a heavily sclerotized embolus (see Fig. 2).

Of the structures making up the male pedipalp, the embolus is the most complex and is species specific. The embolus of the most common American species of *Castianeira, C. longipalpus,* is typical of the vast bulk of the *Castianeira.* The embolus is straight, highly sclerotized, and has a spiral twist at its end (Fig. 10). In some, this terminal twist is barely detectable, e.g., *C. descripta* (Fig. 91), while in others it is very distinct, e.g., *C. cingulata* (Fig. 103). In several species of *Castianeira* the twist is completely dominant and the whole embolus is spirally twisted, e.g., *C. rubicunda* (the type-species), *C. memnonia* (from Panama; Fig. 196), and *C. trilineata* (Fig. 110). Which is the more primitive characteristic—a straight, fairly long embolus or a low, strongly twisted one? Two factors support the latter alternative.

First, a twist is present in most *Castianeira,* though barely perceptible in some (e.g., *C. nanella, C. descripta, C. athena*). These traces of a twist point to the probably vestigal nature of the structure. The lengthening and straightening of the terminal third of the genital bulb of *C. trilineata* (Fig. 110) could produce the emboli observed in *C. longipalpus* and *C. variata* (Fig. 23).

Second, the "primitive" (i.e., complex and low) twist (counterclockwise in the left palpus and clockwise in the right palpus) most clearly exemplified in *C. memnonia* (Fig. 196) is also seen in some species of the distinct genera *Myrmecotypus* (*M. olympus*) and *Myrmecium.* That such complex and homologous structures arose at least three times is highly unlikely. It is more likely that the ancestral palpus had a low twist; in some species, through time, the embolus has lengthened, often to the extent of leaving but a vestige of the twist or no twist at all. Within the *Castianeira* the whole range of palpus evolution is exhibited: *C. memnonia, C. trilineata, C. cingulata, C. longipalpus, C. descripta.* The male genital index (a measure of the elon-

gation of the embolus, a high value representing a highly elongated embolus) is useful in species determination in *Castianeira* but is a poor measure of whether the palpus is advanced or primitive. Such a determination can come only from studying the structure of each tip.

Myrmecotypus has a more varied collection of terminal genital structures than does *Castianeira*, which may suggest a possible polyphyletic origin of the genus. *Myrmecotypus olympus* and *M. rettenmeyeri* have low, spirallike ends, the former with a large sclerotized embolus (Fig. 260) and the latter with a very short embolus (Fig. 262). *M. orpheus* (Fig. 257) and *M. niger* (Fig. 244) have two small terminal projections, clearly a conductor and an embolus in the latter case and probably also in the former. (The embolus is at the distal terminus of the palpal duct.) In *Myrmecotypus* (except *M. pilosus*) there seems to be a general tendency for simplification of the terminal structures instead of a trend towards elongation.

In *Mazax* the embolus is a small, thin, twisted structure in the *spinosa* and *pax* species groups. *Mazax ajax* has a straight, fairly thick embolus without a terminal twist.

Within the genital bulb, the palpal duct (the "receptaculum seminis" of Comstock, 1940) runs down the neck from the embolus and into the globose section, where it makes one or more loops and then proceeds internally (within the genital bulb) and out of view. This basic pattern is typical of all members of the Castianeirinae, but there are some variations of the pattern that are constant within certain taxa and are useful in determining relationships. Old World species of *Castianeira*, *Corinnomma*, and *Merenius* usually have the palpal duct running down the medial side of the genital bulb, making then a single lateral loop. In the New World only *Myrmecotypus pilosus* exhibits this pattern, which suggests an Old World origin of this species. The New World forms usually have more than one loop. All New World *Castianeira* have two loops, one on either side of the descending main palpal duct—a lateral loop and a medial loop (Fig. 2). The lateral loop is larger and extends to the distal portion of the globose section of the genital bulb, while the medial loop is smaller and is limited to the basal half of the globe. The medial loop in *Castianeira trilineata* and *C. memnonia* is very small. *Myrmecotypus niger* also has clear lateral and medial loops (Fig. 243) whereas *M. olympus*, *M. orpheus*, and *M. rettenmeyeri* have two distinct loops *both medial* to the main palpal duct (Figs. 255, 260, 262). This latter pattern is apparently found only in the *olympus* species group of *Myrmecotypus*. The other major neotropical genus of the Castianeirinae, *Myrmecium*, also has two loops in the globe similar to those of *Castianeira*. In *Mazax* two loops are present with the medial loop very small in *M. pax* and the *spinosa* species group, and quite large in *M. ajax*.

In two cases, *C. trilineata* and *M. olympus*, the basal portion of the lateral side of the cymbium bears a spine or spines. In the former species a single heavy spine is present, while in the latter there is a group of spines (Fig. 261). It is possible that this is a unique and primitive character.

In sum, the male genital structure confirms that the subfamily is definitely monophyletic; the common ancestral pedipalp had an embolus similar to that of the present-day *Castianeira memnonia* and a globose genital bulb base containing one or more palpal duct loops. The relatively conservative arrangement of these loops suggests a basic division of the *Castianeira* into a New World group and an Old World group and a polyphyletic origin of *Myrmecotypus*.

Female genital structure. The internal structure of the epigyna of Castianeirinae

is extremely similar throughout the subfamily. The highly sclerotized spermathecae usually have a large anterior section (often globose) narrowing to a posterior neck. Tubelike bursae copulatrices join the spermathecae to the pair of intromittent orifices (Fig. 3). Because the structures are so simple, they are of value as characters only on the highest (evidence of the monophylety of the subfamily) and lowest (diagnostic difference between some species groups in *Castianeira*) levels. There is no clear relationship between the embolus structure of the male and the epigynal structure of the female.

Eye arrangements and sizes. Eye arrangements have long been the basic taxonomic stand-by of arachnologists. They have been considered highly conservative and therefore trustworthy. In the North and Central American Castianeirinae there are three basic eye arrangements and size relationships which belong to the three major genera. *Castianeira*: anterior row moderately recurved; posterior row weakly to moderately procurved; eyes all moderately small to large, sometimes the anterior median eyes larger than the laterals (e.g., *C. memnonia, C. dubia, C. alba,* and *C. rica*). *Myrmecotypus*: anterior row moderately recurved; posterior row recurved; eyes all moderately small, except anterior median eyes twice the diameter of anterior lateral eyes. *Mazax*: anterior row moderately recurved; posterior row approximately straight; eyes moderately large, with the anterior median eyes slightly smaller than the laterals. Many other characters (e.g., thoracic groove, presence of an abdominal petiole, and carapace shape) reinforce the divisions made on the basis of eye characters. This seems to substantiate the value of the eyes as conservative characters.

Cheliceral teeth. The two rows of teeth on the sides of the fang furrow consist of at least two teeth each, but often there is an additional denticle at the distal end of the promargin teeth. This denticle is strong in some, vestigial and almost absent in others. For this reason a strong denticle is considered primitive. In only two species of the North and Central American fauna is this denticle large enough to be considered a tooth: *Castianeira memnonia* and *Myrmecotypus pilosus.* The complete absence of the denticle has occurred independently in several groups of *Castianeira* (e.g., *C. abuelita, C. occidens,* and *C. dorsata*) and in the *fuliginosus* group of *Myrmecotypus.*

Thoracic groove. The thoracic groove or fovea (Fig. 1a) is generally present in *Castianeira* and is always absent in *Myrmecotypus.* In the latter it is usually replaced by a shallow thoracic impression. *Mazax* usually has a weak groove, though it is strong in the atypical species, *Mazax ajax.*

The groove is the external manifestation of an apodeme for the attachment of muscles. The size of the spider may influence the groove's size and depth (larger *Castianeira* generally have stronger grooves), but this does not account for the differences between *Castianeira* and *Myrmecotypus,* which are probably phylogenetic and fundamental.

Mimetic influences. The selection for ant mimicry in spiders influences both their morphology and their behavior, as well as their ecology, habitat preference, and physiology. In the section on methods, the use of certain morphological indices as mimicry indicators is outlined.

Within the Castianeirinae, three of the four genera of North and Central America can generally be distinguished by certain characters resulting from mimetic selection: *Mazax* has a long, rugose abdominal petiole; *Myrmecotypus* has a wide cephalic region; *Sphecotypus* is elongate and has a highly constricted carapace separating a distinct "head." *Castianeira,* containing weak to strong mimics and some non-

mimics, has a more generalized body form, with a cephalothorax and an abdomen without strong constrictions or expansions. Non-mimetic forms of *Castianeira* probably represent the general appearance of the progenitor of the Castianeirinae.

Bicolored carapaces in several species (e.g. *C. cingulata, C. rothi, C. guapa,* and *Mazax xerxes*) give the impression of a "head" separated from a "thorax."

In *Mazax*, the basic mimetic configuration probably coincides with its single origin, i.e., it is probably monophyletic. The mimetic characteristics in *Myrmecotypus* may well be convergent (see *Male genital structure*, above), whereas the generalized characters in *Castianeira* give that genus a general, all encompassing aspect.

Emphasis on characters not influenced by mimicry (e.g., genital structures and thoracic groove) has prevented some polyphyletic groupings—the subfamily is clearly monophyletic—but the vast impact of mimicry has possibly preserved others, e.g., *Myrmecotypus*, and raised bizarre forms to the generic level, e.g., *Sphecotypus*.

Conclusions. From all the characters considered above, two of the three major genera, *Castianeira* and *Mazax*, are probably monophyletic. The coincidence of the peculiar eye arrangements and sizes with the presence of an abdominal petiole confirms *Mazax*'s single origin. *Castianeira* has a generalized appearance and much variability, and although monophyletic, may coincide with the whole subfamily, deriving its monophylety from its all-inclusive quality.

The third major genus, *Myrmecotypus*, appears to be monophyletic when eye, thoracic groove, and mimetic characters are considered, but the great variation in male genital structure suggests a polyphyletic group. Much more study of more extensive collections will be needed to clarify this group; for the time being both convenience and prudence necessitate its unity.

ZOOGEOGRAPHY

The revision is geographically limited to the Nearctic and northern end of the Neotropical faunal regions. The Castianeirinae found in this area accurately reflect the same general faunal region boundaries as those often observed in vertebrate distributions. Except for some Neotropical incursions into southern Texas and Florida (*Castianeira cubana* and *Mazax pax*) and some Nearctic incursions into Cuba (*C. floridana*) and perhaps southern Mexico, most of the species groups are in either the Nearctic or the Neotropical region. The Nearctic region can be divided into two areas: the North Temperate region and the Nearctic deserts. The North Temperate area contains the *longipalpus* (part), *amoena, descripta* (except *C. occidens*), *gertschi, trilineata,* and *cingulata* groups of *Castianeira*. The Nearctic deserts (southwestern U. S. and northwestern Mexico) contain the *dugesii* and *athena* and part of the *longipalpus* and *dorsata* groups of *Castianeira*, as well as *C. occidens*. The Neotropical region includes the *dorsata* (part), *truncata, dubia, alba, similis, memnonia, cubana, peregrina,* and *cincta* groups of *Castianeira*. All *Mazax* and *Myrmecotypus* (except the atypical *Myrmecotypus lineatus*) are Neotropical. The species groups seem to be arranged the same way geographically as they are phylogenetically.

Castianeirinae is predominantly a tropical subfamily and probably originated in the tropics. Limitations both in the scope of this revision and in the collections from tropical South America and Africa prevent determination of the origin and distribution of the subfamily.

Presumably these spiders disperse mainly by ballooning. However, only a few species show wide distributions. Only two species occur in the West Indies (excluding Cuba) —*Mazax spinosa* and *M. chickeringi*, the latter endemic to Jamaica. *Mazax spinosa* on St. Vincent and St. Lucia probably came

through Trinidad and should be considered part of the South American fauna.

INTRASPECIFIC VARIATIONS

In addition to normal color size variations within a population, two types of intraspecific morphological variation are observed in the mature forms of these spiders: sexual and geographic.

Several secondary sexual characters are exhibited. The females are usually larger, have a wider cephalic region and a much smaller abdominal dorsal sclerite than the males. Sexual dimorphism, in conjunction with color and age variations, has been utilized in mimetic polymorphism.

Castianeira cubana and *Mazax pax* both have distinct geographical color forms and could be polytypic species, but this can be determined only when the discontinuities in the collecting have been eliminated. The posterior abdominal red spot in *Castianeira descripta* varies geographically in a cline from a very small spot in the north to a large one in the south and west (see Map 6). Several other species show geographic differences (e.g., abdominal pattern variations in *Castianeira variata* and size differences in *C. longipalpus*), but they are not distinct.

There are several closely related groups of allopatric species that, with further investigation, may turn out to be very variable single species (e.g., *Castianeira crocata-C. floridana, C. descripta-C. occidens-C. walsinghami*, and *C. amoena-C. alteranda*).

Size variations within a single species can be observed in the *Measurements* section under each species, which lists the range of each measurement.

MIMICRY

The ant mimicry exhibited in these spiders ranges from a very generalized sort to species-specific accuracy. The very generalized or familial ant mimics include many of the North American species (e.g., *Castianeira longipalpus, C. cingulata*, and *C. trilineata*), which resemble moderate to large brownish or black ants. A more specialized group is that of the subfamilial and generic ant mimics (e.g., *C. rica* and *C. dubia* in Central America), which are accurate myrmicine or ponerine mimics. Finally, the specific ant mimics (e.g., *Myrmecotypus rettenmeyeri*, a Panamanian spider that resembles *Camponotus serceiventris*) have a single species as their model, and their mimetic modifications are clearly associated with that species.

A stable situation must exist for the more specific forms of mimicry to arise. The mimic must remain temporally and spatially sympatric with the model during the long period of selection for specific mimicry. The tropical forests offer such long range stability, and the most accurate mimics are found there.

Several species are likely mutillid wasp mimics, having red-orange spots or stripes on their abdomens. This coloration has apparently arisen in these species independently (see *Remarks* under *Castianeira dorsata*).

METHODS

The characteristics and measurements (and the indices derived from these measurements) used in describing and comparing the species covered by this revision were chosen using two separate criteria: (1) characteristics that delimit the true or phylogentic differences between taxa (species or genera) or sexes, and (2) characteristics that exhibit the influence of selection for ant mimicry.

The quantitative measurements (listed below) are mainly of the exoskeleton and genital apparatus. With the exception of measurements of the genitalia, they are accurate to 0.05 millimeters. Measurements of the genitalia are accurate to 0.01 millimeters.

A section on Measurements precedes the description of each species. In this section the measurements of the type are presented

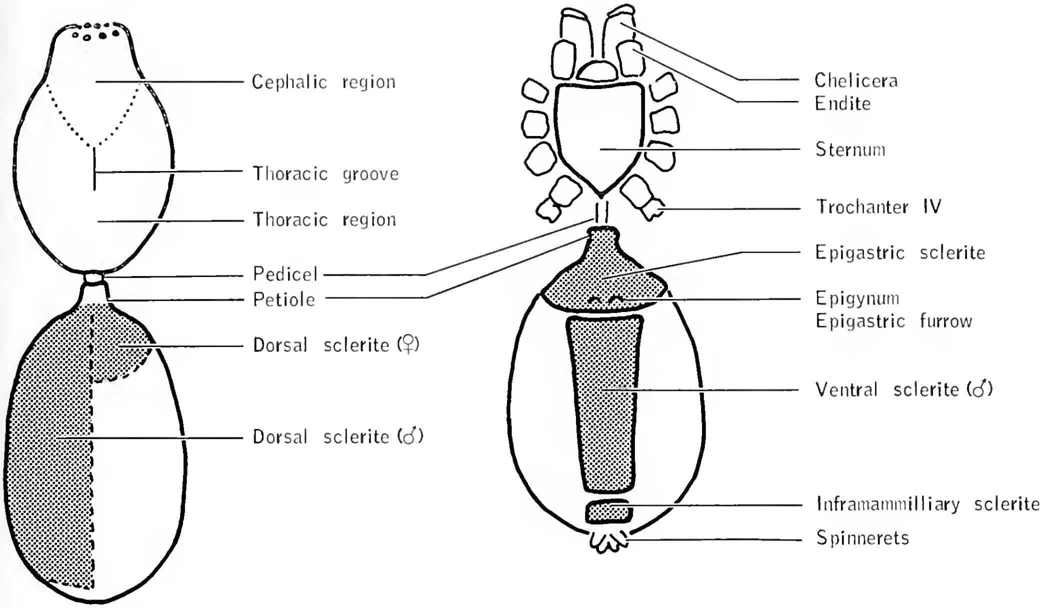

Fig. 1. *Left,* Dorsal view of spider (schematic). *Right,* Ventral view of spider (schematic).

first (if available), followed by the range of the other specimens measured. At least ten males and ten females of each species were measured, when possible, from throughout its geographic range. Averages and associated standard deviations are not meaningful when taken on these diverse samples.

All qualitative characteristics, as well as quantitative characteristics of a discontinuous nature, are included in the section entitled *Description.*

MORPHOLOGY AND MEASUREMENTS

Cephalothorax. The cephalothorax dorsally consists of a shell-like carapace with eight eyes at the anterior end (arranged in two rows), and often a longitudinal thoracic groove; it can be divided into a cephalic region and a thoracic region (Fig. 1a). Ventrally (Fig. 1b) there is a sternum, a labium and its bracketing endites (the coxae of the pedipalps), and a pair of chelicerae. The following measurements on the cephalothorax are reported in this revision:

Carapace length: maximum longitudinal length of the carapace when viewed dorsally from the anteriormost area between the anterior median eyes to the posteriormost point of the carapace.

Carapace width: maximum width of the carapace when viewed dorsally.

Cephalic width: width of the cephalic region of the carapace at the level of the posterior row of eyes when viewed dorsally.

Sternum length: maximum length of the sternum when viewed ventrally. The length includes the posterior sclerotized extension of the sternum found in many species.

Sternum width: maximum width of the sternum (not including extensions of the sternum between the coxae) when viewed ventrally.

From these measurements several proportional indices are derived. Proportional indices are often useful in making objective

comparisons between different individuals in a population or species, or between different species or other taxa, because the emphasis on linear size, which is so variable, is diminished. Variation in the absolute size of a spider is dependent on many environmental conditions (length of growing season, abundance of food, etc.), but the relationships disclosed by the proportions often exhibit the actual phenotypic characteristics. For example, the carapace length of the females of *Castianeira longipalpus* ranges from 2.75 to 4.00 millimeters, but the carapace index (see below) ranges from 66–71, and the smallest and largest specimens have the same carapace index, 66.

The carapace and sternum indices (see below) are derived by dividing the width by the length.[1] Any elongation of these two structures will result in low index values. Because the ants are often thinner than the spiders that mimic them, and thinness and elongation in the spiders often enhance their mimetic resemblance, these two indices can be used as indicators of mimicry, very low values almost always indicating the morphological result of strong selection for mimicry. The following indices are derived from the measurements described above:

Carapace index: carapace width/carapace length × 100. All indices are in the nearest whole unit. A high index value represents a wide carapace, whereas a low index value represents a narrow one. A mimicry indicator.

Cephalic width index: cephalic width/carapace width × 100. This is an index of the narrowness of the head region.

Sternum index: sternum width/sternum length × 100. This is another indication of the degree of elongation in the cephalothorax. A mimicry indicator.

Legs. Many arachnologists report the length of every segment of every leg in the description of a spider. In measuring many hundreds of spiders this task is both tedious and often incomplete (due to the absence of some legs). In addition, within a certain taxon constant size ratios emerge. For example, in the *longipalpus* group of the *Castianeira* the length of femur IV (legs numbered using Roman numerals) is always between 25 and 28 per cent of the length of the whole leg IV, and the length of leg I is between 69 and 75 per cent of the length of leg IV. For these reasons, the only segment of the legs measured was the femur of leg IV, the longest leg segment in these spiders.

Femur IV length: the maximum length of the fourth femur when viewed laterally.

Femur IV width: the maximum width of the fourth femur when viewed laterally. The femur is usually widest at the level of the large dorsal spine near the proximal end of the dorsal edge of the femur, and the measurement includes the tubercle on which the spine is mounted, if it is present.

From these measurements the following indices are derived:

Leg thickness index: femur IV width/femur IV length × 100. A low value indicates a thin leg and a high value a thick one. A mimicry indicator.

Leg length index: femur IV length/carapace length × 100. This is a measure of the general stockiness of the spider, thinner spiders generally having a higher index value, and is therefore somewhat of a mimicry indicator.

Abdomen. The abdomen of the adult always has a dorsal sclerite, fully covering the abdomen in the male but often small or moderately small in the female. Ventrally both sexes have epigastric sclerites (on which the female has its epigynum)

[1] Most of the indices are established so that they result in values below 100 (i.e., the smaller of two measurements divided by the larger). Hopefully these indices will be more easily comprehended than their reciprocals would be.

and often a small inframammilliary sclerite just anterior to the spinnerets. In addition, the male has a ventral sclerite from the epigastric furrow running towards the inframammilliary sclerite (Fig. 16).

The pedicel is the stalk between the cephalothorax and the abdomen and is usually very short and inconspicuous. In some species it is somewhat elongated.

The petiole is the narrowed extension of the abdomen anteriorly. In *Mazax* this is pronounced and heavily sclerotized (a dorsal extension of the epigastric sclerite).

The following measurements on the abdomen have been taken and are reported on in this study.

Abdomen length: maximum length of the abdomen when viewed dorsally.

Abdomen width: maximum width of the abdomen when viewed dorsally.

Dorsal sclerite length: maximum length of the dorsal abdominal sclerite when viewed dorsally. This and the following measurement are almost synonymous with the abdomen length and width in males, where the sclerite is usually full.

Dorsal sclerite width: maximum width of the dorsal abdominal sclerite when viewed dorsally.

Petiole length: maximum length of abdominal anterior petiole when viewed dorsally. This measurement has been taken only on members of the genus *Mazax*.

The following indices are derived from the measurements above:

Abdomen index: abdomen width/abdomen length × 100. This is quite variable in the females. The non-sclerotized (non-rigid) portion of the abdomen varies greatly in size, depending on whether or not the spider is gravid and/or well fed. On the other hand, the abdomens of the males are completely covered by sclerites, and the index values are less variable. This is a good mimicry indicator, especially in the males.

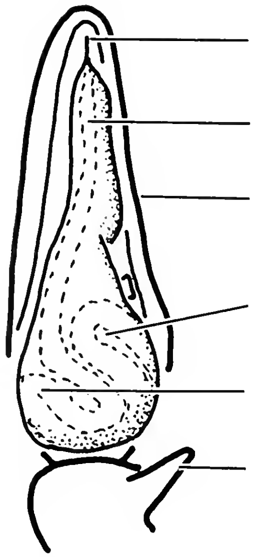

Fig. 2. Left male pedipalp, ventral view. (Genital bulb covered dorsally by the cymbium.)

Dorsal sclerite index: dorsal sclerite width/dorsal sclerite length × 100.

Total length. The total length of a spider can be roughly calculated by adding the abdomen length and the carapace length.

Male genitalia. The separation of species is greatly facilitated by genital characteristics, the structures varying very little within a species.

In the pedipalps of mature male spiders, the tarsal segment is modified as an intromittent organ to hold the sperm. The sperm is emitted from the genital pore (at the center of the epigastric furrow) into a sperm web, taken into the genital bulb, and finally transferred to the epigynum of the female spider in mating. The pedipalps of all males of the Castianeirinae have a large cymbium covering the genital bulb dorsally. The genital bulb has a globular base and a narrower distal neck ending in a sclerotized embolus (Fig. 2). It contains a tubelike coiled canal, the palpal duct. In many, but not all, Castianeirinae the embolus is a fairly straight, highly sclerotized structure. In species having straight emboli

the following useful measurements have been made:

Embolus length: length of highly sclerotized portion of the distal end of the genital bulb when viewed ventrally.

Bulb length: length of entire genital bulb from bottom of globular region to tip of embolus.

And from these two measurements the following index is derived:

Male genital index: embolus length/bulb length × 100. This index is remarkably constant within a species and is not correlated with any epigynal structures.

In the species in which the distal end of the genital bulb is strongly twisted, these measurements and the index derived from them cannot be made (e.g., *Castianeira memnonia*, *C. trilineata*, and several species of *Myrmecotypus*).

The arrangement of loops made by the palpal duct is also constant and invariable and is characteristic of certain taxa (species, species-groups, and genera). In all cases, the palpal duct runs a longitudinal tube towards the embolus from the basal portion of the genital bulb, where there are one or more loops.

Often there is a prolateral, heavily sclerotized tibial apophysis (Fig. 2); this is invariably simple.

In a few, isolated cases, there are heavy spines on the retrolateral base of the cymbium (e.g., *C. trilineata* and *Myrmecotypus olympus*).

Female genitalia. The epigyna of the females of the Castianeirinae are quite simple, with two openings (intromittent orifices) just anterior to the epigastric furrow, opening into a pair of tubelike bursae copulatrices leading to heavily sclerotized spermathecae, usually having an anterior bulb section and a posterior neck section, although the separation of the two sections is often vague and sometimes non-existent. The fertilization tubes leading from the spermathecae to the oviduct arise from the posterior ends of the spermathecae and are not sclerotized (Fig. 3).

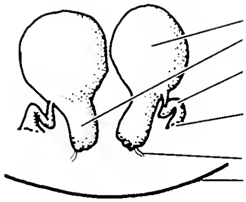

Fig. 3. Internal epigynum, dorsal view.

The shape, size, and direction of the intromittent orifices, the shape of the spermathecae, and the simple convolutions of the bursae copulatrices are often useful specific characteristics.

MORPHOLOGY AND DESCRIPTIONS

The descriptions include the qualitative characteristics (color, general shape, distribution of hair, genital structures, etc.), discontinuous quantitative characteristics (spination, cheliceral teeth, abdominal setae), and some other quantitative characteristics (cephalic width index).

Color. The following range of color is used to describe the spiders: (from lightest to darkest) white, creamy white, yellow-white, yellow, yellow-brown, yellow-orange, orange, orange-brown, red-brown, brown, purple-brown (usually non-sclerotized surfaces), maroon, maroon-brown, brown-black, black. Most of these are modified by using "light," "dark," or "deep." But more important than the precise color is the relative color of different parts—i.e., the pattern. A leg may be described as orange-brown, and vary in the species from yellow-brown to red-brown, but if the tibia or leg I is described as lighter than the tibia of leg IV, it is usually a constant relationship.

Hair and setae. The hairs on the carapace are usually simple, short hairs, although they are often somewhat longer in the cephalic region. Often there are plumose, feather-like hairs (usually making up any longitudinal band of white hairs). The

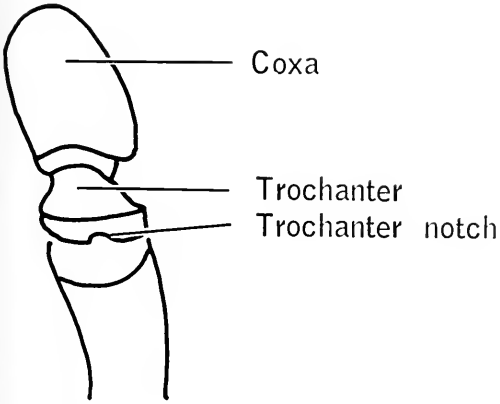

Fig. 4. Trochanter notch.

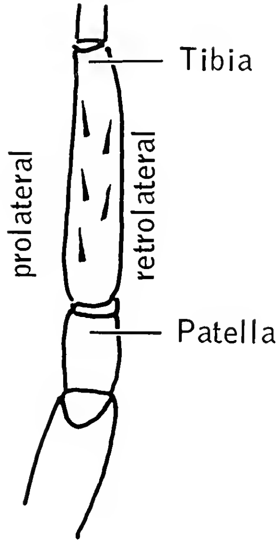

Fig. 5. Tibia I ventral spinotion: 3–2.

hairs of the abdomen are almost exclusively short and plumose. Abdominal hair patterns are often, but not always, reinforced by underlying pigment patterns (as the red abdominal spot in *C. descripta, C. crocata, C. floridana,* and *C. occidens*).

The sternum is usually sparsely covered with long simple hairs or thicker setae (see section on abdominal setae below).

The legs are usually covered with non-erect, simple hairs, and density is expressed as lightly, moderately, or heavily hirsute.

Thoracic groove. The thoracic groove ("fovea" of British arachnologists) (Fig. 1a) is expressed as weak, moderately weak, moderate, moderately strong, or strong, depending on its length and depth. In some taxa it is entirely absent and is often replaced with a poorly defined thoracic impression.

Trochanter IV notch. On the distal, ventral margin of the trochanter (second segment of the leg) there is often a small notch (Fig. 4). This notch is usually rounded and is strong, moderate, weak, or absent.

Sculpture. Sculptural characteristics are not found extensively in the *Castianeira,* but are used in *Mazax,* where great differences in surface textures exist. Surfaces are described as granulose, rugose (full of wrinkles), or smooth.

Spination. The legs are usually quite spiniferous, but the number and positions of the spines are relatively variable within a species. The ventral spination of the tibia of leg I is reported because the spination is fairly constant, easily observable, and often useful in distinguishing between species or species-groups. Of the two numbers in the notation (e.g., see Fig. 5), the first represents the prolateral ventral spines and the second the retrolateral ventral spines. In addition, the spines are described as weak, moderate, or strong (character of thickness), and short, moderately short, moderately long, or long.

Abdominal setae. The abdomen usually has two pairs of setae at its anterior dorsal end—an anterior, or first pair, and a posterior, or second pair (Fig. 6). The first pair is usually thinner than the second. In *Mazax* the second pair is often developed into heavy spines. The setae are described as either hairlike, very thin, thin, moderately thin, moderate, moderately stout, or stout.

Chelicerae and cheliceral teeth. The color of the chelicerae is that of its anterior

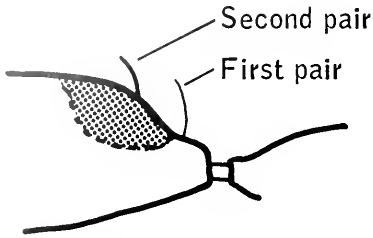

Fig. 6. Abdominal setae (lateral view of anterior abdomen).

surface and is often the same as that of the carapace. The fangs are simple, fairly heavy, and evenly curved.

The cheliceral teeth are in two rows—the promargin teeth and the retromargin teeth. The retromargin teeth are closer to the base of the fang than are the promargin teeth (Fig. 79). Sometimes there is a denticle near the distal promargin tooth. The only difference between a denticle and a small tooth is a difference in size, and it is therefore sometimes a subjective one. In most cases the denticle is clearly a tiny vestige of a functional tooth.

In a few small species of *Castianeira* the apical setae on the promargin of the chelicerae are thickened and serrated, forming a "rake" or heavy claw (Figs. 267, 270, 273).

Eyes. Curvature of the eye rows is determined by observing the carapace dorsally. In recurved row of eyes, the medial eyes are anterior to the lateral eyes; in a procurved row, the medial eyes are posterior to the lateral eyes.

ILLUSTRATIONS

The illustrations were made under a microscope, using different magnifications—15 × for cephalothoraxes, abdomens, and some other large parts, 90 × for male and female genitalia and eyes, and 216 × for embolus tips. The scales of the illustrations for each magnification are constant, thereby facilitating direct comparisons of all homologous structures.

The male and female genitalia of each species are drawn showing (1) the ventral aspect of the male pedipalp and usually the details of the tip of its embolus and (2) an external and internal view of the epigynum (the latter illustration showing the structure cleared in clove oil). No attempt was made to indicate hirsuteness or spination in these drawings.

The abdomens are drawn schematically in Plates IV, VI, IX, XII, XIV, and XIX. The different shadings represent relative hair or pigment colors, with white generally representing either white hair or light pigmentation, grey representing brown, black, or dark hair or dark pigmentation, and horizontal stripes representing yellow, orange, or red-orange hairs or pigmentation. These figures are merely aids to the descriptions and should be used in conjunction with them.

SYSTEM OF CLASSIFICATION

A major objective of this study is the design of a classification that is both natural and highly utilitarian. The emphasis on utility is reflected in a conservative approach to nomenclature and in the use of a simple hierarchy. Within the sub-family, only the categories genus and species are used, with the species arranged in species-groups that reflect their obvious relationships. The use of many categories to illustrate better the relationships among taxa may be very praiseworthy, but is also very risky, especially considering the "immortal" quality of the family-group, genus-group, and species-group names proposed. Only a careful and exhaustive study of an extremely well-collected group (such as the birds or mammals) over its complete range might usefully employ the many categorical subdivisions.

A hierarchy utilizing subfamily, tribe, genus, subgenus, species, and subspecies could be applied to this revision (for instance, the *cinctus* species-group of the *Castianeira* could be considered a subgenus, or the two forms in the variation of *Castianeira cubanus* could be given sub-

specific names), but it would have the weakness of depending on relatively incomplete collections from but a part of the taxon's distribution (in this case a clearly monophyletic, world-wide subfamily). The classification in this revision is both stable and flexible. No restrictive pigeon holes have been created that will hinder future work with the more complete and extensive collections that will be made. The relationships between the taxa studied are stated without petrifying the classification with tribal, subgeneric, and subspecific names.

RECORDS

The complete records for each species are included in the thesis form of this revision (Reiskind, 1967). If the species is widespread, only a general description of its distribution and a map are presented here; if it is more restricted, more specific distribution records are added.

ACKNOWLEDGMENTS

I wish first to thank Dr. Herbert W. Levi of the Museum of Comparative Zoology for his continuous help and encouragement.

The excellent collections in the Museum of Comparative Zoology and the American Museum of Natural History have been invaluable; I would like to thank Dr. Willis J. Gertsch and Mr. W. Ivie of the latter institution for their assistance and for making available to me the excellent collections that they have made over the past thirty years. I am very grateful for the loan of the personal collections of the late Dr. H. Exline (Mrs. D. L. Frizzell), Mr. Vincent D. Roth, and Mr. William B. Peck, which have proved especially valuable. I also wish to thank the following museums (and their curators) for the generous loans of type material used in this work: American Museum of Natural History (Dr. Willis J. Gertsch), the United States National Museum (Dr. Ralph Crabill), the British Museum (Natural History) (Dr. G. O. Evans and Mr. D. Clark), Institut Royal des Sciences Naturelles de Belgique in Brussels (Mr. J. Kekenbosch), the Muséum National d'Histoire Naturelle in Paris (Dr. M. Vachon), the University Museum in Oxford (Dr. G. C. Varley), Senckenbergische Naturforschende Gesellschaft in Frankfurt (Dr. Otto Kraus), the Ohio State University Collection (Dr. C. Triplehorn), and the Kansas State University Collection (Dr. C. Rettenmeyer).

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TAXONOMY

Subfamily *CASTIANEIRINAE* new subfamily

Type-Genus. Castianeira Keyserling 1879.

Characteristics. Two rows of eyes, the posterior row wider than the anterior row; the posterior eyes about equal; the median eyes of the anterior row slightly smaller to much larger than the lateral eyes.

Endites truncated at apex with no depression or constriction in the middle of their ventral faces.

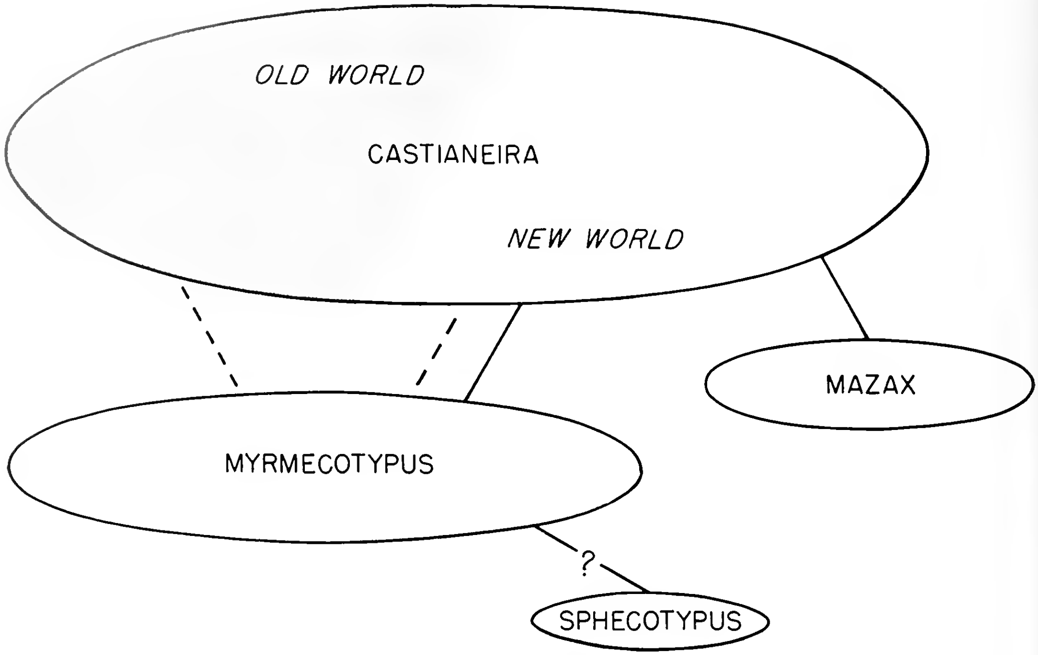

Diagram 1. Origins of the North and Central American Castianeirinae. The solid lines indicate the probable origins, while the dashed lines suggest the possible polyphyletic origins of *Myrmecotypus*.

Carapace and abdomen hairless or covered with simple and plumose hairs but never with iridescent scales.

Female genitalia with a simple pair of epigynal openings; bursae copulatrices leading to heavily sclerotized spermathecae.

Male pedipalp with a large cymbium completely covering the dorsal portion of the genital bulb. The genital bulb with a globular base and always somewhat extended anteriorly with an embolus at its distal end. Palpal duct pattern of one or more loops in the basal portion of the genital bulb.

Anterior spinnerets conical (never cylindrical) and adjacent to one another.

Leg length order usually 4 1 2 3 but sometimes 4 1 3 2.

Distribution. World-wide but predominantly tropical and subtropical.

Diagnosis. Members of this subfamily differ from other members of the Clubionidae in their distinctive male pedipalp and simple epigynal structure. Another distinctive character is the shape of the endites.

Discussion. Justification for the proposal of a new subfamily has been outlined in *Reclassification of the Micariinae*, p. 164.

From the North and Central American representatives of this subfamily, it appears that *Castianeira* is a large, generalized group and that the other genera are specialized groups derived from *Castianeira*. The relationships of the genera in this study (see *Phylogenetic Relationships of the Genera*, p. 167) are summarized in Diagram 1.

Key to North and Central American Genera of Castianeirinae

1a. Abdomen with a distinct, rugose abdominal petiole (Fig. 285); anterior eyes approximately equal or anterior median eyes smaller than laterals .... *Mazax*

1b. Abdomen with a negligible petiole; anterior eyes approximately equal or anterior median eyes larger than laterals 2

2a. Thoracic groove absent (often a depression present); anterior median eyes much larger than anterior lateral eyes 3
2b. Thoracic groove present; anterior median eyes approximately equal to or slightly larger than anterior lateral eyes .... *Castianeira* (except *C. trimac*)
3a. Narrow carapace (carapace index less than 60); posterior eyes recurved .... *Myrmecotypus* or *Sphecotypus*
3b. Wide carapace (carapace index greater than 60); very small; posterior eyes procurved .... *C. trimac*

Castianeira Keyserling

Castianeira Keyserling, 1879, Verhandl. Zool. Botan. Ges. Wien 29:334–335, pl. 4, fig. 28, ♂. Type-species by monotypy: *Castianeira rubicunda* Keyserling, *op. cit.*, 29:335–336, pl. 4, fig. 28, ♂, from New Grenada, northern South America; in the British Museum (Natural History).

Micariaulax Becker, 1879, Ann. Soc. Entomol. Belgium 22:82, pl. 2, figs. 9, 10, ♂. Type-species by monotypy: *Micariaulax dugesii* Becker, *op. cit.*, 22:83, pl. 2, figs. 9, 10, ♂, from Guanajuato, Mexico; in the Brussels Museum, examined.

Tylophora Pavesi, 1880, Ann. Mus. Civ. Genova 15:344–345, ♂, ♀. Type-species by monotypy: *Tylophora antinorii* Pavesi, *op. cit.*, 15:345–347, ♂, ♀, from Ludien near Tozer [Tozeur], Tunisia; in the Genoa Museum.

Thargalia Karsch, 1880, Z. Ges. Naturwiss. 53: 376. Type-species: *Thargalia memnonia* (C. L. Koch).

Geotrecha Emerton, 1889, Trans. Connecticut Acad. Sci. 8(9):168–169. Type-species: *Geotrecha crocata* (Hentz) (see synonymies of *Castianeira descripta*).

Pedo O. P.-Cambridge, 1896, Biol. Centrali-Americana Arachnida 1:219, pl. 26, fig. 14, ♀. Type-species by monotypy: *Pedo ornatus* O. P.-Cambridge, *op. cit.*, 1:220, pl. 26, fig. 14, ♀, from Amula, Guerrero, Mexico; in the British Museum (Natural History), examined.

Characteristics. Two rows of eyes, the posterior row slightly wider than the anterior row; anterior row moderately recurved, the posterior row moderately to slightly procurved; eyes approximately equal but often with anterior median eyes larger than anterior lateral eyes.

Thoracic groove usually present, often strong. Cephalic region of carapace moderately narrow (cephalic width index 47–73, with *C. cubana* accounting for the values over 67).

Tibia I ventral spination 3–3 or less. Trochanter IV notch often present and deep.

Wide range of lengths (carapace length 1.10–5.40 mm) with a carapace index of 54–76 (moderate to wide).

Distribution. Cosmopolitan.

Discussion: The original description of *Castianeira* (Keyserling, 1879) was much more limited in its scope than the one above. The genus is based on a species (*C. rubicunda* Keyserling) closely related to *C. memnonia*, and the generic description specifically mentions that the legs are "slender and spiney" and "the anterior median eyes are considerably larger than the other, rather equal, ones." Since that time the generic limits have been considerably broadened.

Castianeira is a generalized genus. In possessing general characters of carapace shape, thoracic groove, and eye arrangement, it seems to be the group from which many of the more bizarre genera have arisen—e.g., *Mazax* and *Myrmecium*. Within this large, diversified genus in North and Central America certain relationships can be seen. The species groups are the products of the most obvious relationships.

Three species groups in the North American fauna—the *longipalpus*, *amoena*, and *descripta* groups—fall into one major group, with *C. trilineata* and *C. cingulata* set far apart from them, though perhaps close to one another. The *dugesii* and *athena* groups are mainly restricted to the desert region of southwestern U. S. and northern Mexico, and the *dorsata* group resembles the main U. S. forms, though their genitalia are somewhat different.

The *dubia*, *alba*, *similis*, and *memnonia* groups are strictly neotropical; they have large anterior median eyes, and many members are highly modified for mimetic resemblances to ants. The four groups are genitalically quite different from one an-

other, and the determination of relationships is further complicated by their convergence because of selection for mimicry.

The *cubana* and *cincta* groups are small spiders, all with fairly typical genitalia, the *cincta* group having a heavy "rake" on each of the chelicerae. The relationships of these two groups are not clear.

Misplaced and Doubtful Species

Castianeira arizonica Gertsch, 1942, Amer. Mus. Novit. 1195:8, immature ♀, from Phoenix, Arizona; in the American Museum of Natural History, examined = *Micaria arizonica* (Gertsch).

Species whose types were not available and whose descriptions are insufficient for recognition:

Corinna tricolor C. L. Koch, 1842, Die Arachniden 9:24, fig. 707, ♀, from Pennsylvania. This species resembles a *Castianeira crucigera* with a posterior red spot.

Castianeira zionis Chamberlin and Woodbury, 1929, Proc. Biol. Soc. Washington 42:139, pl. 2, fig. 5 (illustrations of plates 1 and 2 reversed), ♀, from Zion National Park, Utah; in the University of Utah Museum, lost. This species belongs to the *longipalpus* group.

Key to the Males of *Castianeira*

1a. Embolus long and straight or slightly curved (male genital index greater than 20); moderately large (carapace length 2.60–4.60 mm), with carapace and abdomen covered with hairs 2

1b. Embolus other than above; either shorter (male genital index less than 20) or not straight 7

2a. Abdomen with black horizontal hair bands and spots on bright orange hair (Fig. 85) 3

2b. Abdomen not as above 4

3a. Thin legs (leg thickness index 25–27) and long embolus (male genital index 25–26) (north central U.S.) .... *alteranda*, p. 206

3b. Stout legs (leg thickness index 32–35) and moderately long embolus (male genital index 21–24) (southern U.S.) .... *amoena*, p. 204

4a. Abdomen with a median and a posterior light spot 5

4b. Abdomen not as above; with white horizontal bands or white hairs on an orange sclerite 6

5a. Embolus very long (male genital index 32–38) (Fig. 139) (Mexico) .... *azteca* p. 234

5b. Embolus moderately long (male genital index 24) (Fig. 147) (El Salvador) .... *stylifera* p. 233

6a. Abdomen with about eight horizontal white hair bands (Figs. 60, 78) (eastern U.S.) .... *variata* p. 197

6b. Abdomen with an orange sclerite covered with white hairs (Mexico, Arizona) .... *dorsata* p. 231

7a. Anterior median eyes distinctly larger than anterior lateral eyes (mostly Neotropical) 8

7b. Anterior median eyes approximately equal to anterior lateral eyes 17

8a. Embolus with a low twist at tip (Fig. 206) (El Salvador) .... *truncata* p. 237

8b. Embolus not as above 9

9a. Carapace wide (carapace index greater than 67) 10

9b. Carapace moderately narrow (carapace index less than 67) 12

10a. Large (carapace length 2.75–3.25 mm) with a white and black hair pattern (Fig. 157) (Costa Rica, Panama) .... *alba* p. 242

10b. Small (carapace length 1.10–1.60 mm); abdominal pattern not as above 11

11a. Carapace yellow-brown, abdomen with a horizontal row of three spots at posterior end (Fig. 269); distinctive genitalia (Fig. 201) (Panama) .... *trimac* p. 256

11b. Carapace dark brown, abdomen with three horizontal bands of white hairs (Fig. 272); distinctive genitalia (Fig. 199) (Panama) .... *dentata* p. 255

12a. Embolus with a small conical tip (Figs. 171, 177) 13

12b. Embolus not as above 14

13a. Embolus distinctly separated from genital bulb neck (Fig. 176) (Mexico) .... *zembla* p. 239

13b. Embolus not as above (Fig. 170) (Mexico, Costa Rica, Panama) .... *dubia* p. 238

14a. Genital bulb with a complex, low, twisted embolus (Fig. 196) (Panama) .... *memnonia* p. 245

14b. Genital bulb not as above 15

15a. Carapace and abdomen elongated and orange (Fig. 188) (Costa Rica, Mexico) .... *rica* p. 240

15b. Abdomen short and oval (Fig. 276) 16

16a. Carapace bicolored (cephalic region yellow, thoracic region dark brown); genital bulb as in Fig. 214 (Panama) .... *guapa* p. 249

16b. Carapace not bicolored; genital bulb

with an extra convolution in the main palpal duct (Fig. 218) (Cuba, Florida, Texas, Panama) .... *cubana* p. 247
17a. Reddish spot on posterior of abdomen (often extending anteriorly) 18
17b. No reddish spot on abdomen 21
18a. Embolus heavy with strong twist at tip (Fig. 43) (Florida, Cuba) .... *floridana*[1] p. 201
18b. Embolus not as above (Figs. 91, 95, 99) .. 19
19a. Longitudinal white hair band on carapace (similar to Fig. 114) (southwestern U.S.) .... *occidens* p. 211
19b. No white hair band on carapace 20
20a. Reddish abdominal spot extending anteriorly as a pair of large spots (Washton, Oregon) .... *walsinghami* p. 213
20b. Reddish abdominal spot but not as above (eastern U.S.) .... *descripta* p. 208
21a. Embolus with a complex terminal twist .. 22
21b. Embolus straight or with a simple terminal bend 23
22a. Distinctive pedipalp (Figs. 102, 103); dark brown-black carapace, strongly striped legs, and two horizontal lines on abdomen (eastern U.S.) .. *cingulata* p. 221
22b. Distinctive pedipalp (Fig. 110); orange or brown carapace, three horizontal bands on abdomen (eastern U. S.) .... *trilineata* p. 219
23a. Abdomen dark with a pattern of black and white plumose hairs (often in horizontal white stripes 24
23b. Abdomen with no such hairs 30
24a. Longitudinal band of white hairs at posterior end of abdomen (often extending anteriorly) 25
24b. Horizontal band of white hairs at posterior end of abdomen (*longipalpus* group, part) 26
25a. Abdominal pattern with a wide longitudinal white hair stripe with two black spots along median (Fig. 86) (southern U.S.) .... *crucigera* p. 214
25b. Abdominal pattern with a series of wide white hair stripes (eastern U. S.) .... *vulnerea* p. 216
26a. Abdomen with separate white hair bands (Fig. 50) (northern and eastern U.S.) .... *longipalpus* p. 186
26b. Abdomen not as above 27
27a. Abdomen with two horizontal white hair bands connected by a longitudinal median stripe (Fig. 76) (California, Oregon) .... *thalia* p. 192
27b. Abdomen not as above 28

[1] No male of *Castianeira crocata* is known, but if found, it would probably key out to *C. floridana*.

28a. Abdomen with two anterior horizontal white hair stripes (connected), then a pair of white hair spots, then a median horizontal white hair band (Fig. 55) (southwestern U.S.) .... *luctifera* p. 190
28b. Abdomen not as above 29
29a. Abdomen with the two anterior white hair bands (connected) followed by several other bands (Fig. 80) (Maryland) .... *alata* p. 188
29b. Abdomen with a series of white hair bands connected along median line (Mexico) .... *plorans* p. 195
30a. Abdomen yellow at anterior end darkening to dark brown at posterior end (eastern U.S.) .... *gertschi* p. 217
30b. Abdomen not as above 31
31a. Carapace very wide (carapace index greater than 70), small (carapace length 1.25–1.45 mm); distinctive genitalia (Fig. 192) (Panama) .... *cincta* p. 253
31b. Carapace narrower (carapace index less than 70) 32
32a. Embolus thin and straight (Figs. 132, 175, 211) 33
32b. Embolus not as above, with a terminal bend (Figs. 126, 128) 35
33a. Abdomen with a distinctive pigment pattern (Fig. 149) (southwestern U. S. and northern Mexico) .... *nanella* p. 225
33b. Abdomen not as above 34
34a. Carapace bicolored with a dark brown cephalic region and orange-brown thoracic region (Arizona) .... *rothi* p. 229
34b. Carapace not bicolored (red-brown) (southern California) .... *athena* p. 228
35a. Embolus with a right angle bend at distal end (Fig. 128) (northern Mexico) .... *dugesii* p. 223
35b. Embolus with a bend less acute (about 45°) (Fig. 126) (southern California) .... *alfa* p. 226

KEY TO THE FEMALES OF *CASTIANEIRA*

1a. Abdomen with dense plumose hair (white, black, yellow to red-orange); eyes approximately equal; moderate to large size (carapace length 2.60–4.55 mm); carapace heavily covered with hairs 2
1b. Not as above; either without plumose hairs, and/or anterior median eyes larger than laterals, and/or very small 25
2a. Abdomen with a longitudinal red-orange to yellow hair band or posterior spot 3
2b. Abdomen not as above, with a posterior white hair band or stripe or orange and black stripes 12
3a. Epigynal openings very small and medi-

ally directed (Fig. 136) (Mexico and southwestern U. S.) .... *dorsata* p. 231
3b. Epigynal openings not as above 4
4a. Abdomen with a wide longitudinal orange to yellow abdominal band spreading to a wide posterior band (Figs. 156, 159); internal epigynum with bursae copulatrices passing over the anterior ends of the spermathecae (Figs. 137, 145) (Mexico and Central America) .. 5
4b. Not as above; a posterior spot or longitudinal band not forming a horizontal posterior band 6
5a. Epigynum with small openings (Fig. 146); yellow abdominal hairs (El Salvador) .... *stylifera* p. 233
5b. Epigynum with larger openings (Fig. 138); orange abdominal hairs (Mexico) .... *azteca* p. 234
6a. External epigynal openings round, small, and posteriorly directed (Figs. 89, 93, 97); internal epigynum with wide spermathecal necks (Figs. 88, 92, 96) (the *descripta* group) 7
6b. External epigynal openings semicircular, moderately large, and posteriorly directed (Figs. 29, 37, 41, 44); internal epigynum with narrow spermathecal necks (Figs. 28, 36, 40, 45) 9
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7b. No discernible band on carapace 8
8a. Abdomen with red-orange hairs extended anteriorly in two large spots (Fig. 122) (Washington, Oregon) .. *walsinghami* p. 213
8b. Abdomen with a posterior red-orange spot often extended anteriorly but not as above (eastern U. S.) (Fig. 121, Map 6) .... *descripta* p. 208
9a. Abdomen with a wide band of red-orange hairs over a black and white pattern (Fig. 75 for black and white pattern) (California) .. *thalia* (red form) p. 192
9b. Abdomen not as above 10
10a. Abdomen with a red-orange median spot (somewhat elongated) (Fig. 58) (Florida, Cuba) .... *floridana* p. 201
10b. Abdomen with a long red-orange band (Figs. 56, 57) 11
11a. Internal epigynum with straight spermathecal necks (Fig. 45) (southern U.S.) .... *crocata* p. 200
11b. Internal epigynum with spermathecal necks turned outward (Fig. 36) (Mexico) .... *venusta* p. 202
12a. Abdomen with a posterior horizontal white hair band .... 13[1]

[1] Also check *C. athena*

12b. Abdomen not as above; posterior longitudinal white stripe or black and orange horizontal stripes or spots 22
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13b. Epigynal openings directed posteriorly (all species are in the *longipalpus* group with very similar epigyna; the species are most easily separated by abdominal pattern) 15
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14b. Abdominal pattern of white hairs in several divided bands (Fig. 158) (Costa Rica, Panama) .... *alba* p. 242
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16a. Abdomen with many wide horizontal bands (eastern U.S.) .... *variata* p. 197
16b. Abdomen not as above 17
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18a. Abdomen with two anterior white hair bands joined and followed by two pairs of white hair spots (Fig. 54) (southwestern U. S.) .... *luctifera* p. 190
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19a. Abdomen with several horizontal white hair bands, the two anterior ones joined, then followed by a series of abbreviated bands (similar to Fig. 80) (Maryland) .... *alata* p. 188
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20a. Abdomen with three horizontal bands, two anterior and one median (Fig. 82) (Mexico and southwestern U. S.) .... *mexicana* p. 195
20b. Abdomen not as above 21
21a. Abdomen with a short longitudinal white hair band at anterior end with a few white hair chevrons along median line (Fig. 74) (Mexico) .... *flebilis* p. 198
21b. Abdomen with a series of five or more horizontal bands (Fig. 77) (Mexico) (possibly *plorans*[1]) .... *lachrymosa* p. 194
22a. Abdomen with orange and black stripes or pairs of spots of plumose hairs (Figs.

[1] Pattern on abdomen of *Castianeira plorans* is unclear, but it possibly keys out to here or has the bands somewhat connected along the median.

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30a. Carapace clearly bicolored with the cephalic region yellow-orange, thoracic region dark brown; carapace length 2.25–2.40 mm (Panama) .... *guapa* p. 249
30b. Carapace not bicolored 31
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31b. Not as above; smaller (2.15–3.90 mm) 32
32a. Epigynal openings a pair of simple horizontal slits (Fig. 195) (Panama) .... *memnonia* p. 245
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34a. Small (carapace length 1.50–1.65 mm) with a row of heavy serrated spines at apex of chelicera (Fig. 267) (Panama) .... *cincta* p. 253
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THE *LONGIPALPUS* GROUP

Characteristics. Moderately large (male carapace length 2.50–3.70 mm; female cara-

pace length 2.75–4.55 mm), with carapace index 63–73. Abdomen completely covered with plumose hairs, often in a black and white striped pattern but sometimes with a red-orange spot or longitudinal stripe. Spermathecae characterized by globose anterior ends, thin posterior necks, and narrow bursae copulatrices. Male genital index 18 or below (with the exception of *Castianeira variata*). Fairly stocky, with the leg thickness index of the females 27–33. Eyes moderately small and equal.

Discussion. This is the largest of the species groups in *Castianeira* and is distributed from Canada to central Mexico. Two subgroups can be distinguished: (1) *C. longipalpus, C. alata, C. luctifera, C. thalia, C. lachrymosa, C. mexicana, C. plorans, C. variata,* and *C. flebilis,* and (2) *C. crocata, C. floridana,* and *C. venusta.* The first group has white hair bands on the abdomen and fairly thin spermatheeal necks; the second has a red-orange band or spot on the abdomen and similar spermathecae.

Hentz (1847) notes that the spots and bands in this species group ". . .are produced by hairs which are quite deciduous, and hence there are many varieties of markings." For this reason and because of the diagnostic importance of the patterns in this group, many specimens are difficult to identify. The banding on the abdomen of spiders reflects their embryonic segmentation (Crome, 1955). The basic pattern, as seen in *Castianeira longipalpus* (Fig. 51), consists of five major horizontal bands: I and II at the anterior end, followed by an often incomplete band III and a strong median band IV, with a final posterior band, P. There are often some minor bands or pairs of spots between bands IV and P. This hair pattern is also observed in other groups—e.g. *C. alba* and *C. dubia.*

This group is apparently quite complex and widespread in Mexico, but small collections and the fragility of the abdominal patterns have prevented proper study of the Mexican members of the group.

Castianeira longipalpus (Hentz)

Frontispiece. Figures 7–10, 50–53. Map 1.

Herpyllus longipalpus Hentz, 1847, Boston J. Nat. Hist. Soc. 5:457, pl. 24, fig. 9, ♀, from Alabama; lost.

Agroeca tristis Keyserling, 1887, Verhandl. Zool. Bot. Ges. Wien 37:436, pl. 6, fig. 11, ♀, from Maryland; in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

Geotrecha pinnata Emerton, 1889, Trans. Connecticut Acad. Sci. 8(9):170, fig. 4, ♂, ♀. Female cotypes from Topsfield, Massachusetts; in the Museum of Comparative Zoology, examined.

Thargalia longipalpus: Marx, 1889, Proc. U. S. Nat. Mus. 12:513.

Thargalia pinnata: Marx, 1889, Proc. U. S. Nat. Mus. 12:514.

Thargalia perplexa Banks, 1892, Proc. Acad. Nat. Sci. Philadelphia 1892:15, pl. 1, fig. 53, ♀, from Ithaca, New York; in the Museum of Comparative Zoology, examined.

Corinna media Banks, 1896, Trans. Amer. Entomol. Soc. 23:66, penultimate ♂, from Olympia, Washington; in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

Corinna pacifica Banks, 1896, Trans. Amer. Entomol. Soc. 23:66. One male and two female syntypes from Olympia, Washington; in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

Castianeira longipalpus: Banks, 1910, Bull. U. S. Nat. Mus. 72:11. Chickering, 1939, Pap. Michigan Acad. Sci. 24(2):60, figs. 24–27, ♂, ♀. Kaston, 1948, Connecticut Geol. and Nat. Hist. Surv. Bull. 70:398, figs. 1403, 1411, 1427, ♂, ♀.

MALE

Measurements. Based on 24 males: carapace length 2.50–3.50 mm; carapace width 1.75–2.40 mm; carapace index 68–73; sternum length 1.05–1.50 mm; sternum width 0.90–1.20 mm; sternum index 77–86.

Femur IV length 1.85–2.65 mm; femur IV width 0.45–0.75 mm; leg thickness index 25–29; leg length index 70–78.

Embolus length 0.13–0.18 mm; bulb length 1.04–1.50 mm; male genital index 11–13.

Description. Carapace red-brown, covered with plumose white hairs; some black and white hairs predominant in head region. Carapace narrow in head region (cephalic width index 47–49) and smoothly truncated

anteriorly. Ocular region darker. Thoracic groove strong.

Abdomen elongated oval, with almost complete, dark red-brown, dorsal sclerite; covered with dense black and white plumose hairs in four main horizontal white hair bands in same pattern as in female (Fig. 50). Epigastric sclerite orange-brown. Elongated rectangular ventral sclerite from epigastric furrow almost to a small inframammilliary sclerite, both red-brown and covered with simple black hairs. Both pairs of abdominal setae very thin.

Sternum dark red-brown, shield-shaped, with sparse, thin setae, heavier setae near edges. Pedicel very short.

Chelicerae brown, with two moderate retromargin teeth and two promargin teeth, the distal one large and the proximal one moderate. A small distinct denticle just distal and medial to the larger promargin tooth.

Coxae all light brown. Trochanter IV with small notch.

Femora of all legs red-brown; rest of legs I and II yellow; of leg III light red-brown; and of leg IV dark red-brown; both ends of tibia IV, and tarsus IV, lighter. Legs moderately hirsute, with black and white hair pattern on femora III and IV and narrow white hair bands at both ends of tibia IV. Tibia I ventral spination: 2–2, moderate, proximal retrolateral spine smaller.

Pedipalp with blunt, short, retrolateral tibial apophysis. Tarsus with globose genital bulb drawn out into long neck with straight, stout, heavily sclerotized embolus with distinct spiral twist at tip (Figs. 9, 10).

FEMALE

Measurements. Based on 34 females: carapace length 2.75–4.00 mm; carapace width 1.85–2.65 mm; carapace index 66–71; sternum length 1.20–1.75 mm; sternum width 1.05–1.40 mm; sternum index 74–89. Femur IV length 2.15–3.10 mm; femur IV width 0.60–0.85 mm; leg thickness index 26–30; leg length index 74–81.

Description. Carapace dark red-brown, with short, slightly plumose black and white hairs, white hairs predominant in head region. Carapace narrow in head region (cephalic width index 55–58) and smoothly truncated anteriorly (Fig. 53). Ocular region darker. Eyes moderately small and equal (Fig. 52). Thoracic groove strong.

Abdomen oval, with small, rounded, red-brown, anterior dorsal sclerite; covered with a black and white pattern of dense hairs on a grey background in four main horizontal white hair stripes—two anterior, the third midway, and the fourth at the posterior end of the abdomen—with several additional narrower bands, one between the second and third main bands and two between the third and posterior bands (Fig. 51). Epigastric sclerite red-brown. Four light, thin, beaded stripes running from epigastric furrow to posterior spiracular furrow, the median two parallel and arising posterior to epigynal openings and laterals from sides of epigastric furrow. Both pairs of abdominal setae very thin.

Sternum red-brown, shield-shaped, with sparse, thin setae. Pedicel very short.

Chelicerae brown, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal smaller than the retromargin teeth. A small, distinct denticle just distal and medial to the larger promargin tooth.

Coxae all light brown. Trochanter IV with a small notch.

Femora of all legs red-brown; rest of legs I and II yellow; of leg III light red-brown; and of leg IV dark red-brown; both ends of tibia IV, and tarsus IV, lighter. Legs moderately hirsute, with black and white hairs on femora III and IV and white hair bands at both ends of tibia IV. Tibia I ventral spination: 2–2, moderate, proximal retrolateral spine smaller.

External epigynum with heavily sclero-

tized borders to the flared openings (Fig. 8). Internal structure heavily sclerotized, with large bulbed spermathecae narrowing posteriorly to a fairly long, narrow, straight neck (Fig. 7).

Diagnosis. Castianeira longipalpus differs from other species in the *longipalpus* group in its distinctive abdominal pattern (Figs. 50, 51), short, thick embolus (Fig. 10), and small epigynal openings (Fig. 8). *Castianeira luctifera* and *C. thalia* both have a male genital index of less than 14, but their abdominal patterns are distinct from those of *C. longipalpus.*

Remarks. Castianeira longipalpus is the most widespread of the American *Castianeira.* There is a fairly large variation in size, with the northern specimens (Ontario) generally smaller than the southern specimens (New York, Kentucky, Illinois).

Natural history. Castianeira longipalpus has been found inhabiting the leaves on the floor of beech-maple forest in Virginia (Elliot, 1930), under dead leaves in dry places on Long Island (Banks, 1895), on the ground, under stones in the prairie of Oklahoma (Banks, Newport, and Bird, 1932), and abundantly in shaded places in the woods of Massachusetts (Montgomery, 1909). Small, immature specimens were found on herbs but larger ones on the ground in the East Central Illinois forest (Jones, 1941). It is also found in the black oak and beech-maple forests of the Chicago area dunes (Lowrie, 1948).

Reproduction probably occurs in early summer (Jones, 1941). Montgomery (1909) observed copulation in *C. longipalpus.* The male mounts the female over her head. "In copulation the male stands over the female, his ventral surface opposed to her dorsal, their body axes obliquely inclined, his head a little to one side of the anterior end of her abdomen. One palpus is inserted at a time." The male mates several times, and the female accepts more than one mate.

The egg case or cocoon is white and disclike. Montgomery (1909) describes the cocoon construction in detail. The female first spins a cocoon base, sweeping her spinnerets slowly from side to side. Onto this base she discharges from her genital aperture a clean globule of viscous liquid, and in this liquid discharges several large eggs. The cover is produced first by carrying thread from the edge of the base onto and across the egg mass and then, after ten minutes, brushing the spinnerets over the surface. The surface is covered with small debris, probably due to its initially slightly sticky surface or some salivary secretion. An identical cocoon-making operation was observed, by the author, in *Mazax pax* in Costa Rica. Montgomery (1909) reports five cocoons of *C. longipalpus* found, two with eight eggs in them and three with nine.

C. longipalpus is found mature in late summer in New England (see *Remarks* under *C. variata*). In western Tennessee it hatches in the last half of August and matures the next year in late June (Gibson, 1947).

Montgomery (1909) observes the resemblance of this species to "the macroergates of a large mound-building ant," finding some of the spiders most abundant within twenty feet of one such nest. He has shown that the ants are not deceived by the spiders, killing them when placed with them. Hentz (1847) merely states that they move with the "rapidity of lightning."

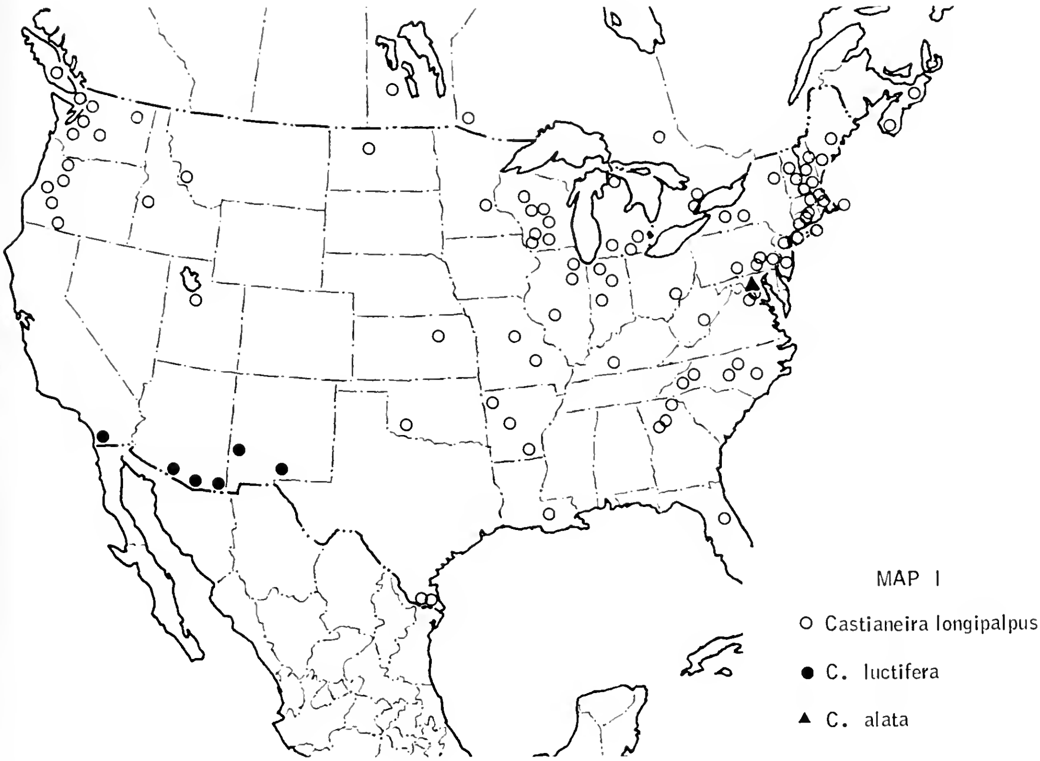
Distribution. Eastern and northern U. S. and southern Canada (Map 1).

Castianeira alata Muma
Figures 15–18, 80. Map 1.

Castianeira alata Muma, 1945, Proc. Biol. Soc. Washington 58:97, pl. 10, figs. 11–13, ♂, ♀. Male holotype from Berwyn, Maryland; in the American Museum of Natural History, examined.

MALE

Measurements. Based on holotype and one male, holotype listed first, range of both follows: carapace length 2.60 mm, 2.60–2.80 mm; carapace width 1.85 mm,



1.85–2.05 mm; carapace index 70, 70–72. Based on holotype only: sternum length 1.30 mm; sternum width 0.95 mm; sternum index 75.

Femur IV length 2.10 mm, 2.10–2.15 mm; femur IV width 0.55 mm, 0.55–0.60 mm; leg thickness index 26, 26–28; leg length index 80, 77–80.

Abdomen length 2.85 mm, 2.85–2.90 mm; abdomen width 1.55 mm, 1.25–1.55 mm; abdomen index 54, 43–54.

Based on one male, not the holotype: embolus length 0.19 mm; bulb length 1.17 mm; male genital index 16.

Description. Carapace red-brown, with white hairs. Eyes small and about equal. Carapace narrower in head region (cephalic width index 48–51) and smoothly truncated anteriorly. Thoracic groove fairly strong.

Abdomen elongated oval, with an almost full, red-brown dorsal sclerite and a white hair pattern—two wide horizontal bands (widening medially and connecting along median), a small horizontal spot, a horizontal chevronlike band, followed by at least two narrower bands and a posterior band (Fig. 80). Epigastric sclerite red-brown. Red-brown ventral sclerite rectangular from epigastric furrow to spiracular furrow. Anterior pair of abdominal setae hairlike, posterior pair thin.

Sternum red-brown. Pedicel negligible.

Chelicerae red-brown, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth; a small denticle just distal and median to the distal promargin tooth.

Coxa I orange-brown, coxae II, III, and IV light yellow-brown. Trochanter IV notch moderately deep.

Femora red-brown (yellow at distal ends). Rest of legs I and II light yellow; rest of leg III yellow, but tibia darker in center and light at ends; rest of leg IV red-brown, with ends of tibia and the tarsus dark yellow. Legs moderately hirsute. Tibia I ventral spination: 2–2, moderately small.

Pedipalp with a strong, blunt tibial apophysis. Tarsus with a globose genital bulb drawn out into a long neck with a straight, thick embolus having a twist at its tip (Figs. 17, 18).

FEMALE

Measurements. Based on one female: carapace length 3.45 mm; carapace width 2.25 mm; carapace index 65; sternum length 1.55 mm; sternum width 1.20 mm; sternum index 79.

Femur IV length 2.60 mm; femur IV width 0.70 mm; leg thickness index 27; leg length index 76.

Abdomen length 4.60 mm; abdomen width 2.65 mm; abdomen index 58; dorsal sclerite width 1.00 mm.

Description. Carapace red-brown, with white hairs. Eyes small and about equal. Carapace narrower in head region (cephalic width index 56) and smoothly truncated anteriorly. Thoracic groove fairly strong.

Abdomen elongate oval, with a small, red-brown dorsal sclerite and a white and brown-black hair pattern—two wide horizontal white bands (connected along median), a small median white spot, five white chevrons decreasing in size posteriorly, and a wide posterior band of white hairs (a total of 9 bands—easily rubbed off). The two wide white hair bands continue onto sides of abdomen. Ventral area with two longitudinal beaded stripes from sides of epigastric furrow to spiracular furrow. Epigastric sclerite orange-brown. Anterior pair of abdominal setae hairlike, posterior pair very thin.

Sternum orange-brown, with thin, sparse setae. Pedicel very small.

Chelicerae red-brown, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth; a small denticle just distal and median to the distal promargin tooth.

Coxa I light red-brown, coxae II, III, and IV light yellow-brown. Trochanter IV notch moderately deep.

Femora red-brown (yellow at distal ends). Rest of legs I and II light yellow; rest of leg III yellow-brown; rest of leg IV red-brown, with both ends of tibia yellow (reinforced with white hairs) and tarsus yellow-brown. Legs moderately hirsute. Tibia I ventral spination: 2–2, moderately small.

External epigynum with flared openings having sclerotized edges (Fig. 16). Internal structure with extremely globose spermathecae narrowing to thin necks posteriorly (Fig. 15).

Diagnosis. Castianeira alata differs from other species in the *longipalpus* group in its distinctive abdominal pattern and male genitalia (the embolus fairly thick, with male genital index 16).

Remarks. This species, one of the large *longipalpus* group, is found only in Maryland, the most restricted distribution of any *Castianeira* in the United States.

Natural history. "Two specimens were found in a house; two under leaves on the ground" (Muma, 1945).

Distribution. Maryland (Map 1).

Records. Maryland. Montgomery Co.

Castianeira luctifera Petrunkevitch
Figures 11–14, 54, 55. Map 1.

Thargalia luctuosa Banks, 1901, Proc. U. S. Nat. Mus. 23:584, pl. 22, fig. 1, ♀, from Santa Rita Mountains, Arizona; in the United States National Museum, examined. (Preoccupied by *Castianeira luctuosa* O. P.-Cambridge, 1898.)

Castianeira luctuosa: Banks, 1910, Bull. U. S. Nat. Mus. 72:11.

Castianeira luctifera Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist. 29:454 (nomen novum for *T. luctuosa* Banks, 1901).

MALE

Measurements. Based on 10 males: carapace length 2.55–2.95 mm; carapace width 1.75–2.05 mm; carapace index 68–71; sternum length 1.10–1.30 mm; sternum width 0.95–1.10 mm; sternum index 81–92.

Femur IV length 1.85–2.30 mm; femur IV width 0.55–0.65 mm; leg thickness index 27–30; leg length index 71–80.

Embolus length 0.11–0.16 mm; bulb length 0.96–1.25 mm; male genital index 11–14.

Description. Carapace red-brown, with sparse light hairs in a median band, especially long hairs in cephalic region and on lateral edges, with some black hairs on sides of carapace. Head narrow (cephalic width index 48–52) and smoothly truncated anteriorly. Ocular area darker. Eyes moderately small and equal. Thoracic groove strong.

Abdomen long oval, with a full, dark maroon dorsal sclerite covered with black and white plumose hairs—anteriorly two broad white horizontal bands joining medially, followed by a pair of round white hair spots and then, midway on abdomen, a band of white hair; broad white hair band at posterior end of abdomen (Fig. 55). Epigastric sclerite red-brown. Rectangular red-brown ventral sclerite from epigastric furrow to a small red-brown inframammilliary sclerite. Anterior abdominal setae very thin, posterior pair slightly stouter.

Sternum shield-shaped, red-brown, with sparse, short, stout setae. Pedicel short.

Chelicerae brown, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth. A small denticle just medial and distal to the larger promargin tooth.

Coxae all yellow. Trochanter IV notch small and curved.

Femora of legs I and II dark yellow, rest of I and II yellow. Femur III yellow-brown, with black and white hairs, rest of III yellow-brown, with yellow tarsi; femur IV deep red-brown, with black and white hairs; patella IV dark red-brown; tibia IV dark red-brown, with light annuli reinforced with white hairs at both ends; metatarsus IV red-brown; tarsus IV dark yellow. Legs moderately hirsute. Tibia I ventral spination: 2–2, moderately small.

Pedipalp with blunt, short tibial apophysis. Tarsus with globose genital bulb drawn out into a long neck, with a straight, stout, heavily sclerotized embolus having a distinct spiral twist at the tip (Figs. 13, 14).

FEMALE

Measurements. Based on holotype and 19 females, holotype listed first, range of all follows: carapace length 3.40 mm, 2.75–3.65 mm; carapace width 2.25 mm, 1.85–2.40 mm; carapace index 66, 63–70; sternum length 1.60 mm, 1.25–1.65 mm; sternum width 1.30 mm, 1.05–1.30 mm; sternum index 82, 77–84.

Femur IV length 2.50 mm, 1.95–2.60 mm; femur IV width 0.75 mm, 0.60–0.80 mm; leg thickness index 30, 28–32; leg length index 73, 70–77.

Based on holotype alone: abdomen length 4.30 mm; abdomen width 2.65 mm; abdomen index 61; dorsal sclerite length 0.95 mm; dorsal sclerite width 1.20 mm; dorsal sclerite index 126.

Description. Carapace red-brown, with sparse light hairs in broad median band, especially long hairs on head region, and with some black hairs on sides of lateral edges. Head narrow (cephalic width index 53–58) and smoothly truncated anteriorly. Ocular area darker. Eyes moderately small and equal. Thoracic groove strong.

Abdomen oval, with a small, red-brown anterior dorsal sclerite. Black and white plumose hair pattern—anteriorly two broad white horizontal bands joining medially, followed by a pair of round white hair spots and then, midway on abdomen, a pair of oval white hair spots; broad white hair band at posterior end of abdomen (Fig. 54). Epigastric sclerite red-brown. Four

light pigmented, thin, beaded stripes running from epigastric furrow to a small orange-brown inframammilliary sclerite, the median two parallel and intermittently arising posterior to epigynal openings, and the laterals parallel and cleanly arising from sides of epigastric furrow. Abdominal setae very thin.

Sternum shield-shaped and red-brown, with sparse, long setae. Pedicel short.

Chelicerae red-brown, with two moderate retromargin teeth, the distal one slightly larger, and two promargin teeth, the distal one larger and the proximal one much smaller than the retromargin teeth. A small but distinct denticle just medial and distal to the larger promargin tooth.

Coxae all yellow. Trochanter IV with small curved notch.

Femora I and II dark yellow, rest of I and II yellow. Femora III and IV yellow-brown, much darker towards distal end, with some black and white hairs; rest of III yellow-brown; patella IV dark red-brown; tibia IV dark brown, with light annuli reinforced with white hairs at both ends; metatarsus IV dark red-brown; tarsus IV yellow-brown. Legs moderately hirsute. Tibia I ventral spination: 2–2, moderately strong.

External epigynum with dark circular openings (Fig. 12). Internal structure heavily sclerotized, with large, bulbed spermathecae narrowing posteriorly to a fairly short, narrow neck (Fig. 11).

Diagnosis. Castianeira luctifera differs from other *longipalpus* group species in its distinctive abdominal pattern (Figs. 54, 55) and external female genitalia (Fig. 12).

Remarks. This species shows relatively little sexual dimorphism except in the abdominal pattern. The abdominal pattern is a very constant character within the range of each sex of the species.

Natural history. Castianeira luctifera is found running over and under dead leaves in the oak forest of the Chiricahua Mountains. The motions are fast and not noticeably ant-like.

The egg case is white and disc-shaped, with orange eggs. One case collected contained 14 eggs.

Distribution. Southern Arizona, New Mexico, and California (Map 1).

Records. Arizona. Cochise Co., Pima Co., Santa Cruz Co. *California.* San Diego Co. *New Mexico.* Catron Co., Otero Co.

Castianeira thalia new species

Figures 28–31, 75, 76. Map 2.

Holotype. Female from Pacific Grove, Monterey Co., California, 3–IV–1960 (W. J. Gertsch, Ivie, Schrammel); in the American Museum of Natural History. The specific name is a noun in apposition after the Muse of Comedy, Thalia.

MALE

Measurements. Based on 4 males: carapace length 2.65–2.85 mm; carapace width 1.85–2.00 mm; carapace index 68–70; sternum length 1.20–1.30 mm; sternum width 1.00–1.10 mm; sternum index 81–86.

Femur IV length 1.95–2.20 mm; femur IV width 0.55–0.60 mm; leg thickness index 24–29; leg length index 72–78.

Abdomen length 2.65–2.80 mm; abdomen width 1.50–1.80 mm; abdomen index 57–66.

Embolus length 0.13–0.14 mm; bulb length 1.12–1.20 mm; male genital index 11–12.

Description. Carapace orange, with some short, light hairs. Eyes bordered with black. Carapace narrow in head region (cephalic width index 48–49) and smoothly truncated anteriorly. Thoracic groove fairly strong.

Abdomen a long oval with a seven-eighths complete maroon dorsal sclerite with a plumose white hair pattern (somewhat rubbed off) of a median and two anterior horizontal bands, all connected by a median longitudinal band, followed by three flattened chevrons and, finally, a posterior, wide, horizontal band (Fig. 76). Epigastric sclerite dark red-brown. Wide, rectangular,

light red-brown ventral sclerite from epigastric furrow almost to dark red-brown inframammilliary sclerite. Anterior abdominal setae long and very thin, posterior pair long and a bit thicker.

Sternum red-brown with sparse setae. Pedicel negligible.

Chelicerae orange-brown with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth. A small denticle distal and medial to the larger promargin tooth.

Coxae all yellow. Trochanter IV notch moderate.

Femora I, II and III yellow, IV dark yellow; rest of legs I and II light yellow; patella-tibia III light yellow, metatarsus and tarsus III light yellow-brown; rest of leg IV light red-brown. Legs moderately hirsute. Tibia I ventral spination: 2–2, moderately small.

Pedipalp with small blunt tibial apophysis. Tarsus with globose genital bulb drawn out into a long neck with short, straight, blunt embolus tip with a clear twist (Figs. 30, 31).

FEMALE

Measurements. Based on holotype and 6 females, holotype listed first, range of all follows: carapace length 2.95 mm, 2.90–3.40 mm; carapace width 1.90 mm, 1.85–2.20 mm; carapace index 65, 65–69; sternum length 1.30 mm, 1.30–1.50 mm; sternum width 1.10 mm, 1.10–1.20 mm; sternum index 87, 83–88.

Femur IV length 2.15 mm, 2.10–2.55 mm; femur IV width 0.60 mm, 0.60–0.75 mm; leg thickness index 28, 28–31; leg length index 74, 72–76.

Abdomen length 2.80 mm, 2.80–4.15 mm; abdomen width 1.80 mm, 1.80–2.80 mm; abdomen index 64, 58–69.

Description. Carapace yellow-brown with median longitudinal light hair band, longer hairs on head region. Eyes bordered with black. Carapace narrow in head region (cephalic width index 54–58) and smoothly truncated anteriorly. Thoracic groove fairly strong.

Abdomen is oval with a small, red-brown dorsal sclerite and a distinctive plumose black and white hair pattern—anterior white hair spot followed by a horizontal white hair band (one fourth distance from anterior end) and another median horizontal stripe. These three areas connected by a median, longitudinal white hair band. The median horizontal stripe is followed by three median, flat chevrons and finally a wide, posterior, white hair band (Fig. 75). Rest of dorsal abdomen covered by black hairs. Epigastric sclerite red-brown. Ventral area with four faint, longitudinal, beaded stripes from epigastric furrow to small orange-brown inframammilliary sclerite. Anterior pair of abdominal setae hairlike, posterior pair very thin.

Sternum light red-brown with sparse, thin setae. Pedicel negligible.

Chelicerae light brown with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth. A small denticle distal and medial to the larger promargin tooth.

Coxae all yellow-white. Trochanter IV notch moderately deep.

Femora of all legs very light brown with dark hairs, especially dense on femur IV. Rest of legs I and II yellow-white, of leg III very light brown, of leg IV light brown with light yellow tarsus. Legs moderately hirsute. Tibia I ventral spination: 2–2, small.

External epigynum with two large, flared openings (Fig. 29). Internal structure with globose spermathecae narrowing to moderately thin, distinct necks posteriorly (Fig. 28).

Diagnosis. Castianeira thalia differs from other *longipalpus* group species in its distinctive abdominal pattern.

Remarks. A single specimen of *C. thalia* from a population in Piercy, California, has a wide band of red-orange hairs overlying

the fundamental black and white hair pattern. Except for this character, the spider is typical of *C. thalia.* This may be an example of an aberrant color form, or perhaps it is part of a polymorphic complex like the one reported in *Enoplognatha ovata* (= *Theridion ovatum*) (Geyer, 1967).

Natural history. Little is known of the habits of *C. thalia,* but one specimen reportedly was collected under a rock. Probably, like most *longipalpus* group species, it prefers running over dead leaves in shade.

Distribution. California and Oregon (Map 2).

Records. California. Los Angeles Co., Mendocino Co., Monterey Co., San Diego Co. *Oregon.* Wallowa Co.

Castianeira lachrymosa (O. P.-Cambridge)
Figures 34, 35, 77. Map 3.

Pedo lachrymosa O. P.-Cambridge, 1898, Biol. Centrali-Americana Arachnida 1:275, pl. 34, fig. 4, ♀, from Amula, Guerrero, Mexico; in the British Museum (Natural History), examined.
Castianeira lachrymosa: O. P.-Cambridge, 1898, Biol. Centrali-Americana Arachnida 1:286.
Castianeira lugens O. P.-Cambridge, 1898, Biol. Centrali-Americana Arachnida 1:288, pl. 32, fig. 10, "♀." Penultimate female holotype from Amula, Guerrero, Mexico; in the British Museum (Natural History), examined. NEW SYNONYMY.

FEMALE

Measurements. Based on one female holotype: carapace length 3.40 mm; carapace width 2.30 mm; carapace index 69; sternum length 1.50 mm; sternum width 1.25 mm; sternum index 83.

Femur IV length 2.60 mm; femur IV width 0.80 mm; leg thickness index 31; leg length index 77.

Abdomen length 3.95 mm; abdomen width 2.65 mm; abdomen index 68; dorsal sclerite width 0.95 mm.

Description. Carapace brown-maroon and covered with white hairs. Carapace moderately narrow in head region (cephalic width index 61) and smoothly truncated anteriorly. Eyes bordered in black and approximately equal. Thoracic groove moderately strong.

Abdomen oval with a small, red-brown dorsal sclerite and a dorsal brown and white hair pattern—a series of about six horizontal median white stripes ending in a posterior white hair band (Fig. 77). (Many hairs rubbed off.) Ventral abdomen light brown. Anterior abdominal setae hair-like, posterior pair extremely thin.

Sternum red-brown with fairly dense, moderately short setae. Pedicel negligible.

Chelicerae dark red-brown with two moderate retromargin teeth and two promargin teeth, the distal one slightly larger and the proximal one slightly smaller than the retromargin teeth.

Coxae all red-brown. Trochanter IV notch fairly strong.

Femora deep maroon-brown; rest of legs I and II yellow-brown; rest of leg III red-brown with distal ends of patella and tibia as well as whole tarsus yellow-brown; rest of leg IV dark red-brown with ends of tibia and the tarsi yellow-brown. Femora with some black and white hairs, legs moderately hirsute.

External epigynum with small, widely spaced openings, heavily sclerotized (Fig. 35). Internal structure with extremely globose spermathecae having posterior thin necks (Fig. 34).

Diagnosis. Castianeira lachrymosa, a Mexican species, differs from other *longipalpus* group species in its abdominal pattern and internal female genitalia.

Remarks. Castianeira lugens is an immature female and is therefore difficult to compare with mature forms, but its similarity in non-genitalic characteristics to *C. lachrymosa,* in addition to its sympatry, have led to its synonymy.

Natural history. Nothing is known of the habits or habitat of this species.

Distribution. Only known from its type locality in Guerrero, Mexico (Map 3).

Records. MEXICO. *Guerrero.*

Castianeira mexicana (Banks)
Figures 32, 33, 82. Map 3.

Thargalia mexicana Banks, 1898, Proc. California Acad. Sci. (3)1(7):228, pl. 13, fig. 38, ♀, from Tepic, Nayarit, Mexico; destroyed.
Thargalia gracilis Banks, 1898, Proc. California Acad. Sci. (3)1(7):229, pl. 13, fig. 29, ♀, from "no locality," presumably in Mexico; destroyed. NEW SYNONYMY.
Castianeira mexicana: F. P.-Cambridge, 1899, Biol. Centrali-Americana Arachnida 2:82.
Thargalia modesta Banks, 1901, Proc. Acad. Nat. Sci. Philadelphia 53:575, pl. 23, fig. 5, ♀, from Albuquerque, New Mexico; in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

FEMALE

Measurements. Based on one female: carapace length 2.85 mm; carapace width 1.95 mm; carapace index 68; sternum length 1.30 mm; sternum width 1.10 mm; sternum index 83.

Femur IV length 2.15 mm; femur IV width 0.60 mm; leg thickness index 27; leg length index 76.

Abdomen length 2.80 mm; abdomen width 1.85 mm; abdomen index 67; dorsal sclerite width 0.85 mm.

Description. Carapace yellow-orange with light, short hair covering. Eyes small, equal, and bordered with black. Carapace narrow in head region (cephalic width index 58) and smoothly truncated anteriorly. Thoracic groove moderately strong.

Abdomen oval with a fairly small, orange, anterior dorsal sclerite and a white and brown-black hair pattern—a horizontal white hair band at anterior base, a spot on each side behind this band, a narrow horizontal white band at middle, and a white band at posterior end (Fig. 82). Epigastric sclerite light brown. Ventral abdomen with two parallel stripes from sides of epigastric furrow almost to spinnerets. Anterior abdominal setae hairlike, posterior pair very thin.

Sternum yellow-white with sparse, thin setae.

Chelicerae yellow with two moderate retromargin teeth and two promargin teeth, the distal larger and the proximal one smaller than the promargin teeth. A very small denticle just medial and distal to the larger promargin tooth.

Coxae yellow-white. Trochanter IV notch moderate.

Femora light yellow. Rest of legs I and II yellow-white; rest of leg III light yellow; rest of leg IV orange with both ends of tibia and the tarsus lighter. Legs fairly heavily hirsute. Tibia I ventral spination: 2–2, moderately strong.

External epigynum with flared, heavily sclerotized openings (Fig. 33). Internal structure with globose spermathecae having thin posterior necks (Fig. 32).

Distribution. Southwestern U. S. and Mexico (Map 3).

Records. New Mexico. Bernalillo Co.
MEXICO. Nayarit.

Castianeira plorans (O. P.-Cambridge)
Figures 24–27, 79. Map 3.

Pedo plorans O.P.-Cambridge, 1898, Biol. Centrali-Americana Arachnida 1:274–275, pl. 33, figs. 10, 11, ♂, ♀. Male holotype from Amula, Guerrero, Mexico; in the British Museum (Natural History), examined.
Castianeira plorans: F. P.-Cambridge, 1899, Biol. Centrali-Americana Arachnida 2:81.

MALE

Measurements. Based on one male holotype: carapace length 2.90 mm; carapace width 1.95 mm; carapace index 67; sternum length 1.25 mm; sternum width 1.05 mm; sternum index 80.

Femur IV length 2.20 mm; femur IV width 0.70 mm; leg thickness index 30; leg length index 77.

Abdomen length 2.95 mm; abdomen width 1.50 mm; abdomen index 51.

Embolus length 0.15 mm; bulb length 1.19 mm; male genital index 12.

Description. Carapace deep red-brown with some white hairs. Head narrow (cephalic width index 52) and smoothly truncated anteriorly. Eyes moderately small,

equal, and bordered in black. Thoracic groove moderately strong.

Abdomen a long oval with an almost full red-brown dorsal sclerite with white hairs in no discernible pattern, but more at anterior end. Epigastric and rectangular ventral sclerites red-brown with some dark hairs. A very small inframammilliary sclerite. First pair of abdominal setae hair-like, second pair thin.

Sternum reddish orange-brown with very sparse setae and some low white hairs.

Chelicerae red-brown, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one much smaller than the retromargin teeth; with a very small denticle just medial and distal to the larger promargin tooth (Fig. 79).

Coxae all orange-brown. Trochanter IV notch moderately deep.

Femora all deep red-brown; rest of legs I and II deep yellow; rest of legs III and IV red-brown, with both ends of tibia IV lighter. Legs fairly heavily hirsute. Tibia I ventral spination: 2–2, very small.

Pedipalp with moderately small, blunt tibial apophysis. Tarsus with globose genital bulb drawn out into a long neck with a stout embolus with a spiral twist (Figs. 26, 27).

FEMALE

Measurements. Based on one female (paratype): carapace length 3.20 mm; carapace width 2.05 mm; carapace index 63; sternum length 1.35 mm; sternum width 1.20 mm; sternum index 88.

Femur IV length 2.40 mm; femur IV width 0.75 mm; leg thickness index 31; leg length index 75.

Abdomen length 4.40 mm; abdomen width 3.10 mm; abdomen index 71; dorsal sclerite length 0.40 mm; dorsal sclerite width 0.80 mm; dorsal sclerite index 192.

Description. Carapace deep red-brown with some white hairs. Head narrow (cephalic width index 60) and smoothly truncated anteriorly. Eyes moderately small, equal, and bordered in black. Thoracic groove moderately strong.

Abdomen a wide oval with a very small, anterior, red-brown dorsal sclerite. A series of faint horizontal white hair bands on brownish abdomen. Epigastric sclerite red-brown. A very small inframammilliary red-brown sclerite. Ventrum with two lines of light beaded stripes from both ends of epigastric furrow towards the spinnerets. First pair of abdominal setae very thin, second pair thin.

Sternum red-brown with sparse, thin setae.

Chelicerae red-brown with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one much smaller than the retromargin teeth; with a very small denticle just medial and distal to the larger promargin tooth.

Coxae orange-brown. Trochanter IV notch moderately deep.

Femora deep red-brown; rest of legs I and II yellow-orange; rest of III red-brown; rest of IV deep red-brown. Legs fairly heavily hirsute with some white hairs. Tibia I ventral spination: 2–2, moderately small.

External epigynum with flared semi-circular heavily sclerotized openings (Fig. 24). Internal structure with globose spermathecae having moderately thick posterior necks (Fig. 25).

Diagnosis. Castianeira plorans differs from most of the other *longipalpus* group species in its series of abdominal stripes; it differs from *C. lachrymosa* in its thicker, straighter spermathecal necks, and from *C. variata* in its short, stocky embolus.

Remarks. This species is one of many of the *longipalpus* group found in Mexico and may be representative of the whole Mexican fauna. O. P.-Cambridge (1899) notes that the males of *C. plorans* alone occur among the numerous females of *C. venusta*, *C. plorans*, and *C. lachrymosa* and that all these species may be varieties of one,

Castianeira venusta. The genital differences seem to preclude such a vast lumping of species, but further collections and studies are needed.

Natural history. Nothing is known of the habits or habitat of this species.

Distribution. Known only from the type locality in Guerrero, Mexico (Map 3).

Records. MEXICO. *Guerrero.*

Castianeira variata Gertsch

Figures 19–23, 60, 61, 78. Map 2.

Castianeira variata Gertsch, 1942, Amer. Mus. Novit. No. 1195:6, fig. 21, ♂, ♀. Male holotype from Cold Spring Harbor, Long Island, New York; in the American Museum of Natural History, examined.

MALE

Measurements. Based on holotype and 9 males, holotype listed first, range of all follows: carapace length 3.10 mm, 2.90–3.50 mm; carapace width 2.00 mm, 1.95–2.20 mm; carapace index 65, 63–67; sternum length 1.40 mm, 1.30–1.60 mm; sternum width 1.05 mm, 1.00–1.10 mm; sternum index 77, 68–78.

Femur IV length 2.40 mm, 2.15–2.60 mm; femur IV width 0.65 mm, 0.60–0.70 mm; leg thickness index 27, 27–28; leg length index 77, 72–79.

Abdomen length 3.30 mm, 3.10–3.75 mm; abdomen width 1.65 mm, 1.50–1.70 mm; abdomen index 50, 44–54.

Embolus length 0.34 mm, 0.31–0.36 mm; bulb length 1.28 mm, 1.20–1.32 mm; male genital index 27, 25–27.

Description. Carapace dark red-brown with white hairs. Eyes about equal and small. Carapace narrower in head region (cephalic width index 50–57) and smoothly truncated anteriorly. Thoracic groove fairly strong.

Abdomen a long oval with a full, maroonish red-brown dorsal sclerite and about eight horizontal bands of white hairs (many rubbed off) (Figs. 60, 78). Epigastric sclerite red-brown. Red-brown ventral sclerite rectangular from epigastric furrow to a small red-brown inframamilliary sclerite. Anterior pair of abdominal setae hairlike, posterior pair very thin.

Sternum red-brown with moderately thin, moderately long setae and short fine setae. Pedicel very short.

Chelicerae dark red-brown with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth; a small denticle just distal and median to the distal promargin tooth.

Coxa I orange-brown, coxae II, III, and IV yellow-brown. Trochanter IV notch moderately deep.

Femora all red-brown (light yellow at distal ends); rest of legs I and II yellow-white; rest of leg III yellow and rest of leg IV red-brown, with both ends of tibia yellow and a yellow tarsus. Legs moderately hirsute with some white hairs on femora. Tibia I ventral spination: 2–2, moderately small, proximal retrolateral spine smaller, sometimes absent.

Pedipalp with a small, blunt tibial apophysis. Tarsus with a globose genital bulb drawn out into a long neck with a long, straight, moderately heavy embolus widening slightly at the end with a terminal twist (Figs. 22, 23).

FEMALE

Measurements. Based on 10 females: carapace length 3.10–4.55 mm; carapace width 2.00–2.85 mm; carapace index 63–67; sternum length 1.40–2.20 mm; sternum width 1.10–1.50 mm; sternum index 67–84.

Femur IV length 2.35–3.45 mm; femur IV width 0.65–1.00 mm; leg thickness index 27–29; leg length index 72–79.

Abdomen length 4.00–6.40 mm; abdomen width 2.40–3.80 mm; abdomen index 54–67; dorsal sclerite width 0.90–1.30 mm.

Description. Carapace dark red-brown with white hairs, longer on head region. Eyes about equal and small. Carapace narrower in head region (cephalic width index 55–63) and smoothly truncated anteriorly. Thoracic groove fairly strong.

Abdomen oval with a small, dark red dorsal sclerite and black and white hair bands (most rubbed off) in nine horizontal white hair bands, with the last a wider posterior band (Fig. 61). Ventral area with two longitudinal beaded stripes from sides of epigastric furrow to a small red-brown inframammilliary sclerite. Epigastric sclerite red-brown. Anterior pair of abdominal setae hairlike, posterior pair very thin.

Sternum red-brown with sparse, thin setae. Pedicel negligible.

Chelicerae dark red-brown with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth; a small denticle just distal and median to the distal promargin tooth.

Coxa I brown, coxa II moderate yellowish brown, coxae III and IV light yellow-brown. Trochanter IV notch moderately deep.

Femora all dark red-brown (light yellow at distal ends); rest of legs I and II light yellow; rest of III light yellow-brown; rest of leg IV red-brown with yellow annuli at both ends of tibia (reinforced with white hair) and light red-brown at center of the metatarsus. Legs moderately hirsute. Tibia I ventral spination: 2–2, moderately small, proximal retrolateral spine smaller.

External epigynum with a pair of low, fairly wide openings (Fig. 20). Internal structure with very wide bursae copulatrices to rounded spermathecae narrowing posteriorly into necks (Figs. 19, 21).

Diagnosis. The long embolus of the male and the wide epigynal openings and very wide bursae copulatrices of the female distinguish *Castianeira variata* from all other *longipalpus* group species.

Remarks. *C. variata* closely resembles *C. longipalpus* in non-genitalic characters. The extreme differences in genitalia may be the result of competitive pressures arising from their close relationship and sympatric distribution. This "character displacement" may have resulted, also, in the temporal separation of the two species (see *Natural history*, below).

There is a great deal of variation in the extent of the abdominal white hair bands in the males, as illustrated in Figures 60 and 78.

Natural history. *Castianeira variata* is found in drier types of woodland and open areas (Fitch, 1963). It runs rapidly and jerkily and in momentary pauses; it has "the peculiar habit of pumping the abdomen up and down with a rhythmic, swaying motion" (Fitch, 1963), which is also observed in *Castianeira alba.*

Mature forms have only been found in early summer in New England and are therefore temporally separated from *Castianeira longipalpus*, a closely related species, which matures in late summer and early fall.

Distribution. New England to Kansas and Louisiana (Map 2).

Castianeira flebilis O. P.-Cambridge
Figures 38, 39, 74. Map 3.

Castianeira flebilis O. P.-Cambridge, 1898, Biol. Centrali-Americana Arachnida 1:286, pl. 32, fig. 8, ♀, from Amula, Guerrero, Mexico; in the British Museum (Natural History), examined.

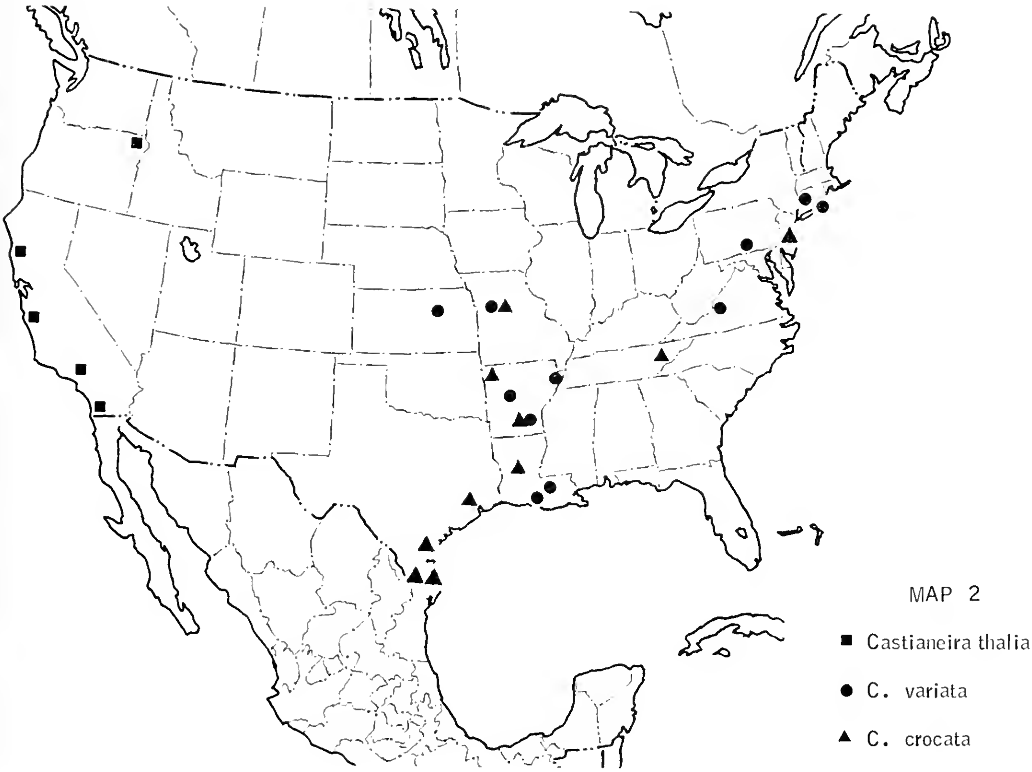
FEMALE

Measurements. Based on one female holotype: carapace length 3.55 mm; carapace width 2.30 mm; carapace index 65; sternum length 1.60 mm; sternum width 1.30 mm; sternum index 84.

Femur IV length 2.75 mm; femur IV width 0.85 mm; leg thickness index 31; leg length index 77.

Abdomen length 3.55 mm; abdomen width 2.10 mm; abdomen index 59; dorsal sclerite width 1.10 mm.

Description. Carapace orange-brown, covered with short, black hairs with some white hairs posterior to the thoracic groove. Carapace moderately narrow in head region (cephalic width index 63) and smoothly but distinctly truncated anteriorly. Eyes



bordered in black. Thoracic groove moderate.

Abdomen oval, with small, light red-brown dorsal sclerite and dorsal black and white hair pattern—median white hair band from anterior end, one-quarter way posteriorly; then from midpoint posteriorly, three horizontal chevrons and a posterior white hair band (Fig. 74). White hair spot on each side of abdomen. Ventrum light yellow with no markings. Abdominal setae very thin, anterior pair thinner.

Sternum red-brown with long setae, especially at edges. Pedicel very short.

Chelicerae light brown, with two moderate retromargin teeth and two promargin teeth; the distal larger and the proximal much smaller than the retromargin teeth, with a small denticle just distal to the larger promargin tooth.

Coxae all light brown. Trochanter IV notch moderate.

Femora medium brown; rest of legs I and II light yellow; rest of leg III dark yellow; rest of leg IV yellow-brown, with ends of tibia and the tarsus slightly lighter. Legs moderately hirsute with some black and white hairs on the femora.

External epigynum with heavily sclerotized, flared openings (Fig. 39). Internal structure of basic inverted pear-shape with thick necks (Fig. 38).

Diagnosis. *Castianeira flebilis* differs from other members of the *longipalpus* group species in its abdominal pattern and extremely thick spermathecal necks.

Remarks. Part of the Mexican fauna, *C. flebilis* is very different from other species collected in Amula.

Natural history. Nothing is known of the habits and habitat of this species.

Distribution. Only known from the type locality in Guerrero, Mexico (Map 3).

Records. MEXICO. *Guerrero.*

Castianeira crocata (Hentz)

Frontispiece. Figures 44, 45, 56. Map 2.

Herpyllus crocatus Hentz, 1847, Boston J. Nat. Hist. Soc. 5:457, pl. 24, fig. 8, ♂, from Alabama; lost.

Liocranum crocatus: Marx, 1883, Araneina, *in* Howard, L. O., A List of the Invertebrate Fauna of South Carolina, Charleston, p. 23.

Thargalia crocata: Marx, 1889, Proc. U. S. Nat. Mus. 12:513.

Castianeira crocata: Banks, 1910, Bull. U. S. Nat. Mus. 72:11.

FEMALE

Measurements. Based on 11 females: carapace length 3.30–4.55 mm; carapace width 2.15–3.15 mm; carapace index 61–70; sternum length 1.50–1.95 mm; sternum width 1.20–1.60 mm; sternum index 79–85.

Femur IV length 2.50–3.40 mm; femur IV width 0.75–1.05 mm; leg thickness index 29–31; leg length index 73–78.

Abdomen length 3.30–5.90 mm; abdomen width 1.95–4.50 mm; abdomen index 52–82; dorsal sclerite width 0.85–1.30 mm.

Description. Carapace dark maroon with short whitish hair. Carapace narrow in head region (cephalic width index 52–60) and smoothly truncated anteriorly. Eyes fairly small and equal. Thoracic groove moderately strong.

Abdomen oval with a small, anterior, maroon dorsal sclerite and a pattern of red-orange and black plumose hairs—a wide median stripe of bright red-orange from just posterior to the sclerite to just anterior of the spinnerets (Fig. 56), rest of abdomen covered with black hairs. Epigastric sclerite red-brown. Ventrum with two faint, light, longitudinal stripes from epigastric furrow to near the spinnerets. Small red-brown inframammilliary sclerite. First pair of abdominal setae hairlike, second pair thin.

Sternum red-brown with long, thin setae. Short pedicel.

Chelicerae red-brown with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth; a very small denticle just medial and distal to the larger retromargin tooth.

Coxae all orange-brown. Trochanter IV notch moderate.

Femora all dark reddish brown. Rest of legs I and II yellow-brown; the patella and proximal ends of the tibia darker; rest of III and IV red-brown with dark yellow tarsi. Tibia I ventral spination: 2–2, moderate.

External genitalia with a pair of oval openings (Fig. 44). Internal structure with extremely globose spermathecae having narrow, posterior necks (Fig. 45).

Diagnosis. Castianeira crocata differs from other *longipalpus* group species in its long, abdominal, red-orange stripe and globose anterior spermathecae with very distinct thin necks. *C. floridana* has a smaller abdominal spot and less of a distinction between globe and neck in the spermathecae. *C. venusta* has a longer stripe and an outward turn of the spermathecal necks. *C. crocata* differs from the *descripta* group in its female genitalia (Figs. 44, 45).

Remarks. Castianeira crocata has often been synonymized with *C. descripta*, whose striking abdominal pattern is superificially similar. Banks (1916) clearly saw the distinction when he recognized "the true *crocata*" as a southern form and the northern "*crocata*" as *C. descripta*. The female genital structure distinctly separates the two species.

No males are definitely associated with this species, but the male of *C. floridana* is probably very close to the hypothetical *C. crocata* male.

Natural history. While this species is found predominantly in southern U. S., it broadly overlaps *C. descripta*, with which it is often confused, and it is possible that references to "*C. descripta*" in Oklahoma and possibly Nebraska refer to this species (see *Natural history*, under *Castianeira*

descripta). Hentz (1847) notes, "This species inhabits houses, hiding in cracks, under boards, etc." This is possibly a mutillid wasp mimic.

Distribution. Southern New Jersey to Missouri and south to Texas (Map 2).

Castianeira floridana (Banks)

Figures 40–43, 58, 59. Map 3.

Thargalia floridana Banks, 1904, Proc. Acad. Nat. Sci. Philadelphia 56:124, pl. 7, fig. 11, imm. ♀. Penultimate female holotype from Punta Gorda, Florida; in the Museum of Comparative Zoology, examined.

Castianeira floridana: Banks, 1910, Bull. U. S. Nat. Mus. 72:11.

Castianeira cubana Bryant, 1940, Bull. Mus. Comp. Zool. 86(7):446, pl. 17, figs. 228, 232, ♂, ♀. Male holotype from Soledad, Cuba; in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

MALE

Measurements. Based on 5 males: carapace length 2.60–3.15 mm; carapace width 1.80–2.15 mm; carapace index 68–70: sternum length 1.20–1.45 mm; sternum width 1.05–1.10 mm; sternum index 77–87.

Femur IV length 1.95–2.30 mm; femur IV width 0.60–0.75 mm; leg thickness index 30–33; leg length index 73–77.

Abdomen length 2.65–3.65 mm; abdomen width 1.50–1.80 mm; abdomen index 49–60.

Embolus length 0.15–0.16 mm; bulb length 0.91–1.19 mm; male genital index 13–18.

Description. Carapace deep red-brown, almost maroon, covered with short white hairs, longer hairs on cephalic region. Head narrow (cephalic width index 48–52) and smoothly truncated anteriorly. Eyes moderately small, equal, and bordered in black. Thoracic groove moderately strong.

Abdomen elongated oval with a full, dark red-brown dorsal sclerite, lighter spot with bright orange hair at posterior end, and covered with black and white hairs—white hairs in two wide horizontal bands, followed by a thinner horizontal band at the midline, followed by two more, thinner, bands (Fig. 59). Epigastric and almost full ventral sclerites dark red-brown. Small brown inframammilliary sclerite. First pair of abdominal setae thin and long, second pair moderate.

Sternum shield-shaped with sparse, fairly short, thin setae. Pedicel short.

Chelicerae red-brown, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one much smaller than the retromargin teeth; with a very small denticle just medial and distal to large promargin tooth.

Coxae all deep orange-brown. Trochanter IV notch moderately small.

Femora all red-brown. Rest of legs I and II deep yellow-brown; rest of legs III and IV red-brown, with tarsi of all legs yellow-brown. Legs moderately heavily hirsute. Tibia I ventral spination: 2–2, moderately small.

Pedipalp with a blunt, short tibial apophysis. Tarsus with a globose genital bulb drawn out into a long neck with a straight, fairly stout, heavily sclerotized embolus having a distinct spiral twist at the tip (Figs. 42, 43).

FEMALE

Measurements. Based on 6 females: carapace length 3.15–3.60 mm; carapace width 2.10–2.50 mm; carapace index 63–70; sternum length 1.50–1.70 mm; sternum width 1.10–1.30 mm; sternum index 75–81.

Femur IV length 2.30–2.80 mm; femur IV width 0.70–0.85 mm; leg thickness index 29–33; leg length index 70–78.

Abdomen length 3.50–4.65 mm; abdomen width 2.05–3.20 mm; abdomen index 57–69; dorsal sclerite length 0.60–0.85 mm; dorsal sclerite width 0.85–1.20 mm; dorsal sclerite index 130–180.

Description. Carapace deep red-brown with sparse, short, white hairs. Head narrow (cephalic width index 55–62) and smoothly truncated anteriorly. Eyes quite small, equal, and bordered in black. Thoracic groove moderately strong.

Abdomen a wide oval with a small, dark red-brown anterior dorsal sclerite. Covered with brownish hairs with a large bright median spot (both orange hairs and light pigmentation) just posterior to the midline (Fig. 58). Epigastric sclerite orange-brown. Four light pigmented, thin, beaded stripes running from epigastric furrow to area just anterior to the spinnerets, the two lateral stripes clearer than the median pair. First pair of abdominal setae very thin, second pair slightly thicker.

Sternum shield-shaped and red-brown with sparse, thin setae. Pedicel short.

Chelicerae red-brown with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one much smaller than the retromargin teeth; with a very small denticle just medial and distal to large promargin tooth.

Coxae all deep yellowish brown. Trochanter IV notch moderate.

Femora all red-brown (hind pair darker). Rest of legs I and II light yellow-orange; rest of leg III yellow-brown and of leg IV red-brown, with both tarsi yellow-orange. Legs moderately hirsute. Tibia I ventral spination: 2–2, moderately small.

External epigynum with heavily sclerotized semicircular openings (Fig. 41). Internal structure heavily sclerotized, with a rounded bulb drawn posteriorly into a long thin neck (Fig. 40).

Diagnosis. C. floridana differs from other *longipalpus* group species having red-orange hair on the abdomen by the restriction of this hair to a median spot in the female and a distinct black, white, and red hair pattern in the male. The female epigynum is also distinct from that of *C. crocata.*

Remarks. This species is allopatric with *C. crocata,* to which it is closely related. The distinct genitalic and pattern differences, however, probably justify its specific rank. The Cuban form has a slightly longer embolus (male genital index 18) than the Floridian form (male genital index 13–14) but agrees in all the other characters. *Castianeira cubana* Bryant is not only the synonym of *C. floridana* but also the junior homonym of *C. cubana* (Banks).

Natural history. Nothing is known of the habits or habitat of this species. It is possible that this is a mutillid mimic.

Distribution. Southern Florida and Cuba (Map 3).

Castianeira venusta (Banks)
Figures 36, 37, 57. Map 3.

Pedo ornatus O. P.-Cambridge, 1896, Biol. Centrali-Americana Arachnida 1:220, pl. 26, fig. 14, ♀. Female syntypes from Amula, Guerrero, Mexico; in the British Museum (Natural History), examined. Female lectotype chosen. A secondary junior homonym of *Herpyllus ornatus* Hentz.

Pedo plumosus O. P.-Cambridge, 1898, Biol. Centrali-Americana Arachnida 1:242–243, pl. 31, fig. 12, ♀, from Amula, Guerrero, Mexico; in the British Museum (Natural History), examined. (Not *Corinna plumosa* Thorell, 1881.) NEW SYNONYMY.

Thargalia venusta Banks, 1898, Proc. California Acad. Sci. (3)1(7):227, pl. 13, fig. 35, ♀, from San Miquel, Sonora, Mexico; destroyed.

Castianeira ornata: F. P.-Cambridge, 1899, Biol. Centrali-Americana Arachnida 2:81.

Castianeira plumosa: F. P.-Cambridge, 1899, Biol. Centrali-Americana Arachnida 2:81.

Castaneira venusta: Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist. 29:456.

Castianeira pedo Roewer, 1951, Abhandl. Natur. Verhandl. Bremen 32(2):446 (*nomen novum* for *Pedo plumosus* O. P.-Cambridge). NEW SYNONYMY.

FEMALE

Measurements. Based on lectotype and 2 females, lectotype listed first, range of all follows: carapace length 3.30 mm, 3.30–3.40 mm; carapace width 2.20 mm, 2.20–2.30 mm; carapace index 67, 65–69; sternum length 1.45 mm, 1.45–1.60 mm; sternum width 1.20 mm, 1.20–1.30 mm; sternum index 85, 81–85.

Femur IV length 2.60 mm, 2.60–2.65 mm; femur IV width 0.75 mm, 0.75–0.80 mm; leg thickness index 29, 29–31; leg length index 78, 75–79.

Abdomen length 4.60 mm, 4.30–4.60 mm; abdomen width 2.90 mm, 2.80–2.90 mm;

abdomen index 63, 63–66; dorsal sclerite length (lectotype not included) 0.60–0.65 mm; dorsal sclerite width 0.95 mm, 0.95–1.00 mm; dorsal sclerite index (lectotype not included) 150–172.

Description. Carapace deep red-brown, covered with short black hairs. Carapace moderately narrow in head region (cephalic width index 60) and smoothly truncated anteriorly. Eyes bordered in black and almost equal, the anterior lateral eyes slightly larger than the anterior median eyes. Thoracic groove moderate.

Abdomen oval, with a small red-brown dorsal sclerite and a dorsal hair pattern—two short horizontal bands of white hair at anterior end (over sclerite), followed by a wide, longitudinal band of orange hairs on light pigment running full length to just before posterior, where it ends in a narrow, horizontal white hair band (Fig. 57). Two large white hair spots on each side of abdomen. Ventral abdomen light brown, with two longitudinal beaded lines of light pigment running from sides of epigastric furrow almost to spinnerets. Abdominal setae very thin.

Sternum deep red-brown with long setae, especially at edges. Pedicel negligible.

Chelicerae brown with two moderate retromargin teeth and two promargin teeth; the distal larger and the proximal smaller than the retromargin teeth (trace of vestigial denticle).

Coxae all light brown. Trochanter IV notch moderately strong.

Femora dark brown. Rest of legs I and II yellow; rest of legs III and IV brown, with lightened areas reinforced by light hair at distal end of patella III, proximal end of tibia III, both ends of tibia IV and tarsus IV. Legs moderately hirsute.

External epigynum with heavily sclerotized, flared openings (Fig. 37). Internal structure with globose spermathecae having narrow posterior necks turned outwards (Fig. 36).

Remarks (see *Remarks* under *C. plorans*).

White spots on side of abdomen sometimes absent.

Natural history. Nothing is known of the habits or habitat of this species.

Distribution. Mexico, and reported by O.P.-Cambridge (1899) from Guatemala (Map 3).

Records. MEXICO. *Guerrero. Sonora.*

The *amoena* Group

Characteristics. Moderately large (male carapace length 2.60–3.55 mm; female carapace length 3.15–4.30 mm;), with carapace index 63–70. Abdomen completely covered with plumose hairs with black horizontal stripes and pairs of spots on a bright orange background. Spermathecae with globose anterior ends, moderately thin posterior necks, and wide bursae copulatrices. Male genital index 21–26, with slightly curved emboli. Eyes moderately small and equal.

Discussion. This group is closely related to the *longipalpus* group, but its distinctive genitalia and patterns easily distinguish it.

Castianeira amoena (C. L. Koch)

Figures 70–73, 84, 85. Map 4.

Corinna amoena C. L. Koch, 1842, Die Arachniden 9:21–22, fig. 705, ♀, from "Carolina"; lost.

Herpyllus ornatus Hentz, 1847, Boston J. Nat. Hist. Soc. 5:456, pl. 24, fig. 6, ♀, from North Carolina; lost.

Herpyllus marmoratus Hentz, 1847, Boston J. Nat. Hist. Soc. 5:458, pl. 24, fig. 10, ♂, from Alabama; lost.

Castianeira amoena: Banks, 1910, Bull. U.S. Nat. Mus. 72:11 (= *ornatus*, = *marmoratus*). Bishop and Crosby, 1926, J. Elisha Mitchell Sci. Soc. 41(3–4):185, pl. 23, fig. 34, ♂.

MALE

Measurements. Based on 10 males: Carapace length 2.60–2.95 mm; carapace width 1.75–2.05 mm; carapace index 66–70; sternum length 1.10–1.30 mm; sternum width 0.95–1.05 mm; sternum index 80–83.

Femur IV length 1.80–2.15 mm; femur IV width 0.60–0.75 mm; leg thickness index 32–35; leg length index 68–72.

Abdomen length 2.70–3.50 mm; abdomen width 1.45–1.90 mm; abdomen index 50–57.

Embolus length 0.23–0.26 mm; bulb length 1.01–1.19 mm; male genital index 21–24.

Description. Carapace dark orange with light orange hairs; narrow in head region (cephalic width index 49–53) and smoothly truncated anteriorly. Ocular region much darker. Eyes moderately small and equal. Thoracic groove moderate.

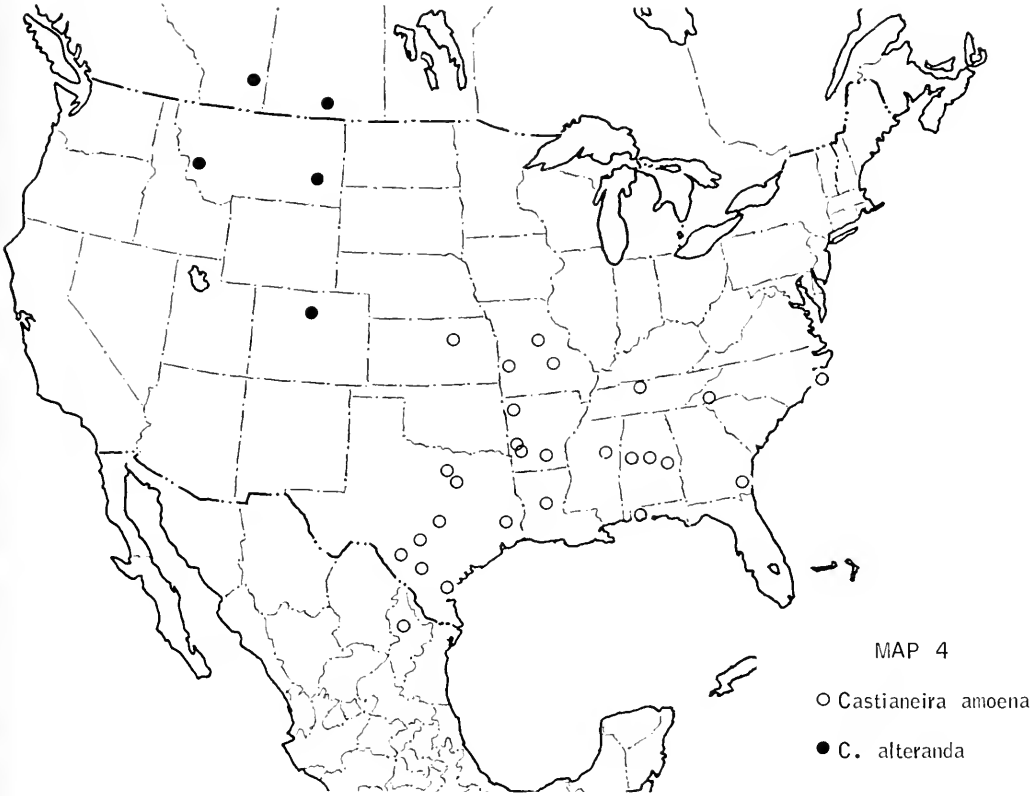
Abdomen oval, with an almost complete maroon dorsal scutum with about seven horizontal black pigment bands on it, the posterior couple missing the median section (Fig. 85). Dark orange hairs arise from darker areas and light yellow hairs arise from lighter areas. Orange hairs predominate on sides and posterior. Epigastric sclerite red-brown. Rectangular, dark red-brown ventral sclerite from epigastric furrow posteriorly about four-fifths distance to posterior spiracular furrow and covered with plumose white hairs. Very small, red-brown inframammilliary sclerite. Both pairs of abdominal setae very thin.

Sternum orange-brown with sparse, thin setae. Short pedicel.

Chelicerae dark red-brown, with two moderate retromargin teeth and two promargin teeth, the distal one large and the proximal one similar to retromargin teeth. A small denticle distal to larger promargin tooth.

Coxa I brown; II, III, and IV light brown. Trochanter IV with a moderate notch.

Femora I and II dark brown, rest of legs I and II light yellow. Femora III and IV orange-brown, with broad, dark brown hair and pigment rings at distal ends (with light tip). Patellae and tibiae of III and IV each with a light ring at each end (especially strong in tibia IV). Rest of III dark yellow. Metatarsus IV dark brown with faintly lighter central annulus, and tarsus IV yellow. Legs moderately hirsute. Tibia I ventral spination: 2–1, moderate.



Pedipalp with slight tibial apophysis. Tarsus with globose genital bulb drawn out into long neck with a fairly thin, slightly curved, sclerotized embolus (Figs. 72, 73).

FEMALE

Measurements. Based on 10 females: carapace length 3.15–3.55 mm; carapace width 2.10–2.35 mm; carapace index 65–68; sternum length 1.40–1.50 mm; sternum width 1.10–1.25 mm; sternum index 77–85.

Femur IV length 2.20–2.50 mm; femur IV width 0.70–0.80 mm; leg thickness index 32–33; leg length index 65–74.

Abdomen length 3.45–4.50 mm; abdomen width 1.85–2.95 mm; abdomen index 53–65; dorsal sclerite width 1.20–1.30 mm.

Description. Carapace bright orange with orange hairs; narrow in head region (cephalic width index 56–58) and smoothly truncated anteriorly. Ocular region much darker. Eyes moderately small and equal. Thoracic groove fairly weak.

Abdomen oval, with a moderate, anterior, light orange dorsal sclerite; horizontal, alternating black and white, plumose hair bands complete and fairly wide anteriorly, becoming thinner and missing median sections posteriorly; orange plumose hairs in a posteriorly widening and darkening band, starting at sclerite and replacing areas of white hairs. Total of about eight black hair bands or pairs of black hair spots (Fig. 84). Epigastric sclerite yellow. Ventral abdomen white. Both pairs of abdominal setae very thin.

Sternum light yellow, with sparse, long, thin setae. Short pedicel.

Chelicerae yellow-brown, with two moderate retromargin teeth and two promargin

teeth, the distal one large and the proximal one similar to retromargin teeth. A small denticle distal to the larger promargin tooth.

Coxae all light yellow. Trochanter IV with a deep notch.

Femora I and II dark brown (covered with dark dense hairs), tips of femora and rest of legs I and II yellow-white. Femora III and IV yellow-orange, with broad, dark brown hair rings at distal ends (but with white tip). Patellae and tibiae of III and IV each with a broad white hair (and light pigment) ring at each end. Rest of III dark yellow. Metatarsus IV dark brown, with faintly lighter central annulus, and tarsus IV dark yellow. Legs moderately hirsute. Tibia I ventral spination: 2–2, moderate (proximal retrolateral spine smaller).

External genitalia with a pair of flat oval openings (Fig. 71). Internal structure with globose spermathecae narrowing gradually to posterior necks (Fig. 70).

Diagnosis. Castianeira amoena differs from *C. alteranda* in its stocky legs (leg thickness index 32–35) as well as some differences in its abdominal pattern.

Remarks. (See *Remarks* under *Castianeira alteranda.*)

Natural history. Castianeira amoena, mainly a southern species, is found in the non-forest maritime communities of North Carolina (Barnes, 1953a and 1953b) and under rock and stones and on stone outcrops in eastern Nebraska (Worley and Pickwell, 1931). Hentz (1847) reports the species "wandering on paths, and very active, in woods or unfrequented places."

Distribution. Southeastern U.S. (Map 4).

Castianeira alteranda Gertsch

Figures 66–69, 83. Map 4.

Castianeira alteranda Gertsch, 1942, Amer. Mus. Novit. No. 1195:6, figs. 19–20, ♂, ♀. Male holotype from Hamilton, Ravalli Co., Montana; in the American Museum of Natural History, examined.

MALE

Measurements. Based on holotype and one male, holotype listed first, range of both follows: carapace length 3.55 mm, 3.30–3.55 mm; carapace width 2.35 mm, 2.15–2.35 mm; carapace index 66, 66; sternum length 1.60 mm, 1.50–1.60 mm; sternum width 1.20 mm, 1.15–1.20 mm; sternum index 78, 78.

Femur IV length 2.80 mm, 2.40–2.80 mm; femur IV width 0.70 mm, 0.65–0.70 mm; leg thickness index 25, 25–27; leg length index 78, 74–78.

Abdomen length 3.85 mm, 3.30–3.85 mm; abdomen width 2.15 mm, 1.70–2.15 mm; abdomen index 56, 52–56.

Embolus length 0.34 mm, 0.31–0.34 mm; bulb length 1.34 mm, 1.24–1.34 mm; male genital index 26, 25–26.

Description. Carapace orange, with very short orange hairs. Eyes small, about equal, and bordered in black. Carapace narrower in head region (cephalic width index 52–55) and smoothly truncated anteriorly. Thoracic groove moderately strong.

Abdomen oval with a seven-eighths full red-brown dorsal sclerite covered with orange-white and black hairs in obscure bands (most rubbed off). Epigastric sclerite red-brown. Ventral, elongate, orange-brown, rectangular sclerite running from epigastric furrow almost to spiracular furrow. A small orange inframammilliary sclerite. Anterior abdominal setae thin, posterior pair stouter.

Sternum orange, covered with sparse, small, thin orange setae. Pedicel very small.

Chelicerae orange, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one slightly smaller. A small denticle distal to larger promargin tooth.

Coxae dark yellow-orange. Trochanter IV notch moderate.

Femora red-brown. Rest of legs I and II yellow-brown; rest of leg III deep red-brown (patella lighter); rest of leg IV dark red-brown (patella and both ends of tibia

lighter). Tibia I ventral spination: 2–2, small, proximal retrolateral spine smaller than the rest.

Pedipalp with a moderate pointed tibial apophysis. Tarsus with a globose genital bulb drawn out into a long neck with a long, slightly curved, and fairly thick embolus (Figs. 68, 69).

FEMALE

Measurements. Based on 2 females: carapace length 3.65–4.30 mm; carapace width 2.30–2.80 mm; carapace index 63–65; sternum length 1.65–1.85 mm; sternum width 1.30–1.45 mm; sternum index 79–80.

Femur IV length 2.95–3.30 mm; femur IV width 0.70–0.85 mm; leg thickness index 24–26; leg length index 77–81.

Abdomen length 4.20–5.65 mm; abdomen width 2.10–3.65 mm; abdomen index 50–64; dorsal sclerite width 1.05–1.10 mm.

Description. Carapace dark yellow with low orange hairs. Eyes fairly small, equal, and bordered in black. Carapace narrows in head region (cephalic width index 61–62) and is smoothly truncated anteriorly. Thoracic groove moderately strong.

Abdomen oval with a small, orange, anterior dorsal sclerite and a black and orange dorsal hair pattern (the orange becoming white on sides of abdomen) of three wide horizontal orange bands joined broadly along the median, followed by two thin horizontal bands and a wide band just anterior to the spinnerets (Fig. 83). Yellow epigastric sclerite. Ventral abdomen with two parallel white stripes from ends of epigastric furrow posterior to the spinnerets. Anterior abdominal setae thin, posterior pair stouter.

Sternum yellow-orange with long, thin setae. Pedicel very small.

Chelicerae yellow-orange, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one slightly smaller. A small denticle distal to larger promargin tooth.

Coxae dark yellow (IV slightly darker). Trochanter IV notch moderately strong.

Femora all yellow-orange. Rest of legs I and II very light yellow; rest of leg III yellow-orange, with metatarsus and tarsus yellow-brown; rest of IV yellow-orange, with tarsus brown and ends of tibia very light yellow with white hairs. Legs moderately hirsute. Tibia I ventral spination: 2–1, small.

External epigynum with two oval openings (Fig. 66). Internal structure with somewhat globose spermathecae with moderately wide necks posteriorly and wide bursae copulatrices (Fig. 67).

Diagnosis. Castianeira alteranda differs from *C. amoena* in its moderately thin legs (leg thickness index 24–27), as well as in having some differences in its abdominal pattern.

Remarks. C. alteranda is similar to *C. amoena* but slightly larger, with longer, thinner legs and emboli. The two groups are entirely allopatric and may be the extremes of a geographic cline, but until intermediates are found, they should be considered separate species.

Natural history. Nothing is known of the habits of this species.

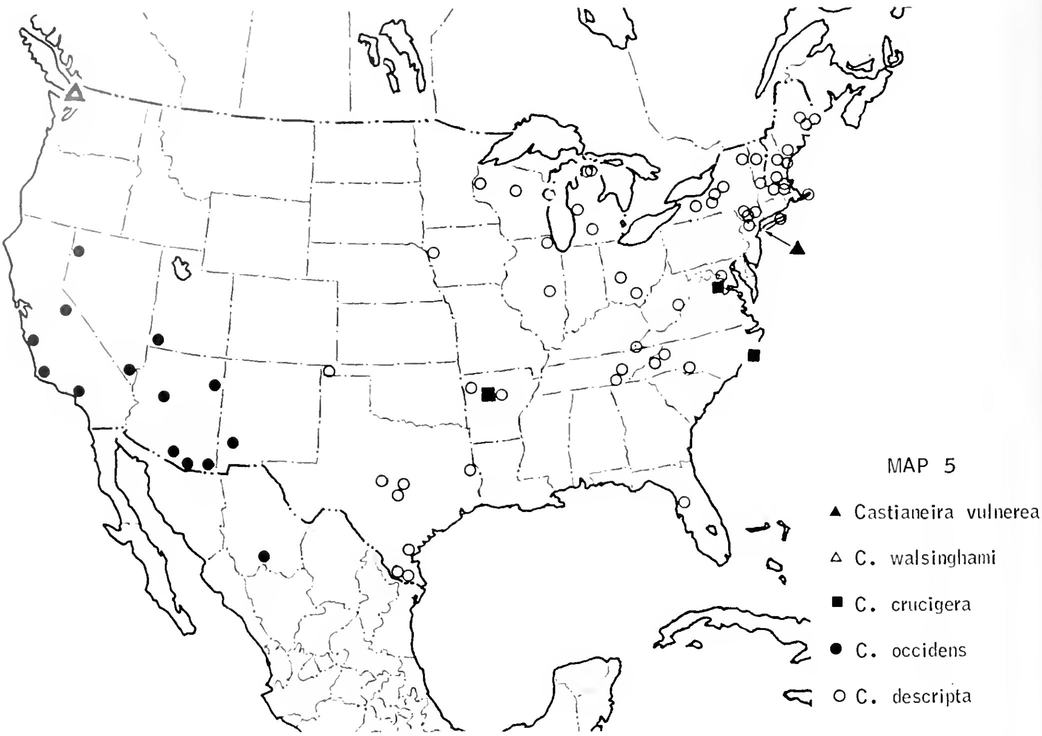
Distribution. Montana, Colorado, Alberta, and Saskatchewan (Map 4).

Records. CANADA. *Alberta. Saskatchewan.*

Colorado. Boulder Co. *Montana.* Custer Co., Ravalli Co.

THE *DESCRIPTA* GROUP

Characteristics. Moderately large (male carapace length 2.10–3.70 mm; female carapace length 2.60–4.05 mm), with a carapace index 63–72. Abdomen covered with plumose hairs with a red-orange posterior spot, often extending considerably anteriorly and laterally, or a white hair pattern. Spermathecae with globose anterior ends and thick, slightly twisted posterior necks. Epigynal openings small and round. Male genital index 15–18, with fairly thin emboli. Moderately stocky, with the leg thickness



index of the females 25–31. Eyes moderately small and equal.

Discussion. This group is closely related to the preceding two species groups, but the distinctive female genitalia clearly differentiates it. Two sub-groups can be distinguished: (1) *C. descripta, C. occidens,* and *C. walsinghami,* and (2) *C. crucigera* and *C. vulnerea.* The first group has an abdominal red-orange posterior spot, while the second group has a white hair pattern concentrated along the midline of the abdomen. The three species in the first group are allopatric, closely related, and may all be part of one polytypic species, but they are separated, conditionally, on the basis of their pattern differences and slight genitalic differences.

Castianeira descripta (Hentz)
Figures 88–91, 121. Maps 5, 6.

? *Sphasus vittatus* Walckenaer, 1837, Histoire Naturelle des Insectes Aptères 1:378 (Abbot, 1792, Spiders of Georgia fig. 369, examined). *Nomen oblitum.*[1]

Herpyllus descriptus Hentz, 1847, Boston J. Nat. Hist. Soc. 5:456, pl. 24, fig. 7, ♀, from North Carolina; lost.

Geotrecha crocata: Emerton, 1889, Trans. Connecticut Acad. Sci. 8(9):171, pl. 3, fig. 3, ♂, ♀. Emerton, 1902, The Common Spiders of the United States, Boston, p. 7, figs. 20–22, ♂, ♀.

Thargalia agilis Banks, 1892, Proc. Acad. Nat. Sci. Philadelphia 1892(1):15, fig. 52, ♀, from Six Mile Creek, near Ithaca, New York; in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

Thargalia fallax Banks, 1892, Proc. Acad. Nat. Sci. Philadelphia 1892(1):16, pl. 1, fig. 54, ♂. Male syntypes from Ithaca, New York; in the Museum of Comparative Zoology, examined.

Thargalia crocata: Banks, 1892, Proc. Acad. Nat. Sci. Philadelphia 1892(1):17.

Castaneira descripta: Simon, 1897, Histoire Naturelle des Araignées, II, fasc. 1:158, figs. 161, 162, ♂. Comstock, 1912, The Spider Book, Ithaca, New York, p. 578, figs. 656, 657.

[1] This name has gone unused since Walckenaer's description (1837), except in a review of Walckenaer's work by Chamberlin and Ivie (1944).

Castianeira descripta: Chickering, 1939, Pap. Michigan Acad. Sci. 24(2):59, figs. 20–23, ♂, ♀. Kaston, 1948, Connecticut Geol. and Nat. Hist. Surv. Bull. 70:395, figs. 1402, 1409–1410, 1426, ♂, ♀.

MALE

Measurements. Based on 11 males: carapace length 2.90–3.70 mm; carapace width 1.95–2.40 mm; carapace index 65–68; sternum length 1.25–1.65 mm; sternum width 1.05–1.30 mm; sternum index 77–86.

Femur IV length 2.20–2.85 mm; femur IV width 0.60–0.75 mm; leg thickness index 26–28; leg length index 73–81.

Embolus length 0.15–0.19 mm; bulb length 0.93–1.10 mm; male genital index 15–17.

Description. Carapace red-brown, covered with short black and white hairs. Carapace narrow in head region (cephalic width index 53–58) and smoothly truncated anteriorly. Ocular region darker. Eyes small and equal. Thoracic groove strong.

Abdomen oval, with an almost full, dark red-brown dorsal sclerite covered with fine hair—red-orange hairs on redder posterior half and extending anteriorly onto red-brown ground. Some white hairs at anterior end. Epigastric and ventral sclerite red-brown. Ventral sclerite elongated rectangle, almost extending to a small orange-brown inframammilliary sclerite. First pair of abdominal setae thin, second pair moderately thin.

Sternum dark red-brown, shield-shaped, with sparse, thin setae. Pedicel very short.

Chelicerae red-brown with two moderately large retromargin teeth and two promargin teeth, the distal one larger and the proximal smaller than the retromargin teeth. A small denticle medial and distal to the larger promargin tooth.

Coxae all orange-brown. Trochanter IV notch moderate.

Femora all dark red-brown. Rest of legs I and II yellow; of leg III orange-brown; of leg IV red-brown, with a yellow-brown tarsus. Legs moderately hirsute. Tibia I ventral spination: 2–2, moderate.

Pedipalp with a short, blunt tibial apophysis. Tarsus with a globose genital bulb drawn out into a long neck with a straight, thin embolus, twisted at the tip (Fig. 90, 91).

FEMALE

Measurements. Based on 15 females: carapace length 3.30–3.95 mm; carapace width 2.10–2.60 mm; carapace index 63–67; sternum length 1.45–1.80 mm; sternum width 1.15–1.55 mm; sternum index 79–86.

Femur IV length 2.45–3.10 mm; femur IV width 0.70–0.90 mm; leg thickness index 25–31; leg length index 71–83.

Description. Carapace red-brown, covered with short black and white hairs. Carapace narrow in head region (cephalic width index 57–61) and smoothly truncated anteriorly. Ocular region darker. Eyes moderately small and equal. Thoracic groove moderately strong.

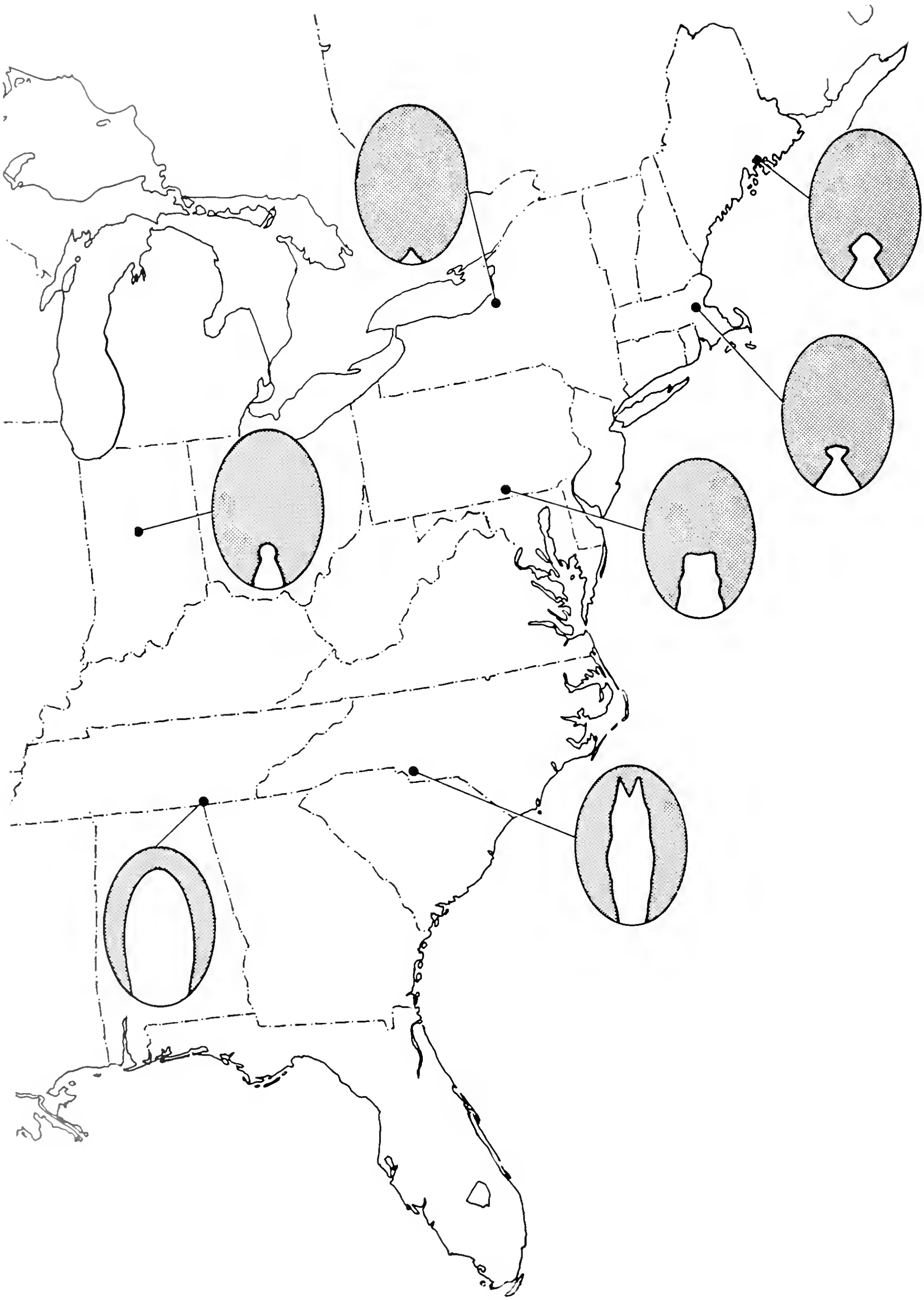
Abdomen oval, with a very small, rounded, anterior, red-brown dorsal sclerite and covered with dark brown or brown-black hairs, with a wide red spot at posterior end narrowing anteriorly, resulting in a bright red-orange posterior wedge (Fig. 121). Epigastric sclerite red-brown. Two light pigmented, thin, beaded stripes from lateral sides of epigastric furrow posteriorly towards spinnerets. First pair of abdominal setae very thin, second pair thin.

Sternum as in male.

Chelicerae dark red-brown with two moderately large retromargin teeth and two promargin teeth, the distal one large and the proximal smaller than the retromargin teeth. A small distinct denticle medial and slightly distal to the larger promargin tooth.

Coxae all red-brown. Trochanter IV notch moderate.

Femora all red-brown. Rest of legs I and II deep yellow; of legs III and IV with patella-tibia striped red-brown with two



lateral dorsal yellow stripes, metatarsi red-brown, tarsi yellow brown. Legs moderately hirsute. Tibia I ventral spination: 3–2, moderate (proximal prolateral spine much smaller than the rest).

External epigynum with two widely separated, small, circular openings (Fig. 89). Internal structure heavily sclerotized with saclike spermathecae narrowing only slightly posteriorly (Fig. 88).

Diagnosis. Castianeira descripta can be distinguished from other *descripta* group species by its posterior red spot (sometimes very small) and the absence of a white longitudinal stripe on the carapace.

Remarks. This wide-spread American species shows geographic variation in the size of its posterior red spot, which increases in size towards the south and west (see Map 6). This seems to be a smooth cline, and while there is a good deal of variation within each area, there is no evidence of any polymorphism.

This species is not closely related to *Castianeira crocata* (see *Remarks* under *C. crocata*).

Natural history. Castianeira descripta is found in forest litter, beneath logs and stones and among leaves on the ground in Michigan (Chickering, 1939), commonly on the ground in dry fields and pastures in Ohio (Barrows, 1918), on the ground and under stones in the prairie of Oklahoma (Banks, Newport and Bird, 1932), on dusty roads and under boards in Nebraska (Worley and Pickwell, 1931), and on straw washed up by the tide in Nantucket (Emerton, 1930). Generally *C. descripta* is found in more open ground than are *C. longipalpus* and *C. cingulata.* It feeds on small insects, and has no special prey (Bilsing, 1920).

Montgomery (1909) noted the similarity of the method of copulation of *C. descripta* to that of *C. longipalpus* (see *Natural history* under the latter species).

The egg case is like that of *C. longipalpus,* a white disc. One egg case from Ithaca, New York (August 5), contained 22 eggs; Kaston (1948) reports one (August 30) with 14 eggs; and Fitch (1963) reports two, one with 26 eggs and one with 19.

Scheffer (1906) notes that ". . . from its general appearance and movements this spider might, at first sight, be easily mistaken for a velvet ant (mutillid)." Fitch (1963) describes the jerky, darting movements and the devious course of the foraging spider.

Distribution. Eastern U.S. (Map 5).

Castianeira occidens new species

Figures 96–99, 113–115. Map 5.

Holotype. Male from Lakeside, Navajo Co., Arizona, 8-VII-1940 (Gertsch and Hook); in the American Museum of Natural History. The specific name is a noun in apposition meaning the West.

MALE

Measurements. Based on holotype and 4 males, holotype listed first, range of all follows: carapace length 3.10 mm, 3.10–3.55 mm; carapace width 2.05 mm, 2.05–2.35 mm; carapace index 67, 65–68; sternum length 1.40 mm, 1.35–1.60 mm; sternum width 1.10 mm, 1.10–1.30 mm; sternum index 81, 81–88.

Femur IV length 2.60 mm, 2.60–2.90 mm; femur IV width 0.65 mm, 0.65–0.80 mm; leg thickness index 25, 24–28; leg length index 81, 80–86.

Abdomen length 3.55 mm, 3.55–4.20 mm; abdomen width 1.75 mm, 1.55–2.25 mm; abdomen index 49, 46–55.

Embolus length 0.17 mm, 0.17–0.20 mm; bulb length 1.03 mm, 1.03–1.16 mm; male genital index 17, 16–17.

←

Map 6. Abdominal pattern variation in *Castianeira descripta.* (The white area on each represents the red-orange posterior spot.)

Description. Carapace red-brown and covered with dense hairs—a wide longitudinal median band of white hairs, with dark hairs on the sides, and the thoracic region bordered with white hairs. Head narrow (cephalic width index 53–58) and smoothly truncated anteriorly. Small lighter spot just anterior to thoracic groove. Eyes moderately small, equal, and bordered in black. Thoracic groove moderate.

Abdomen a long oval with a full dorsal sclerite, at anterior end red-brown with white hairs but becoming orange with bright orange hairs on posterior three-fourths of abdomen, with a tongue of anterior coloration extending posteriorly along the median to the middle of the abdomen (Fig. 113). Epigastric sclerite orange-brown, and an almost full orange ventral sclerite. First pair of abdominal setae very thin, second pair thin.

Sternum shield-shaped and orange-brown, with moderately sparse setae.

Chelicerae red-brown, with two moderate retromargin teeth and two promargin teeth, the distal larger and the proximal smaller than the retromargin teeth. No distinct denticle present.

Coxae all yellow-orange. Trochanter IV notch moderate.

Femora all red-brown, with some black and white hairs. Rest of legs I and II yellow; rest of III—patella-tibia light red-brown, metatarsus and tarsus yellow; rest of IV red-brown, except tarsus yellow. Tibia I ventral spination: 3–2, moderate except proximal prolateral spine small. Legs fairly heavily hirsute.

Pedipalp with a short, blunt tibial apophysis. Tarsus with a globose genital bulb drawn out into a long neck with a moderately long, thin, and straight embolus (Figs. 98, 99).

FEMALE

Measurements. Based on 10 females: carapace length 3.15–4.00 mm; carapace width 2.15–2.75 mm; carapace index 65–71; sternum length 1.50–1.75 mm; sternum width 1.20–1.50 mm; sternum index 82–88.

Femur IV length 2.75–3.20 mm; femur IV width 0.70–0.90 mm; leg thickness index 25–30; leg length index 77–87.

Abdomen length 3.95–6.35 mm; abdomen width 2.25–3.95 mm; abdomen index 54–75; dorsal sclerite length 0.30–0.65 mm; dorsal sclerite width 0.75–1.05 mm; dorsal sclerite index 113–290.

Description. Carapace orange-brown and covered with dense hairs—a moderately wide, longitudinal, median band of white hairs with dark hairs on the sides, and the thoracic region bordered with a thin band of white hairs (Fig. 114). Head narrow (cephalic width index 56–61) and smoothly truncated anteriorly. Eyes moderately small, equal, and bordered in black. Thoracic groove moderately strong.

Abdomen oval, with a small, red-brown dorsal sclerite and covered with dense hairs—two abbreviated horizontal white hair stripes surrounded by black hairs at anterior end, followed by a wide median stripe of brilliant orange hairs with black hairs on both sides (Fig. 115). Epigastric sclerite yellow. Ventrum cream colored with dark hairs. First pair of abdominal setae very thin and long, second pair thin.

Sternum shield-shaped, light brown, with thin setae.

Chelicerae red-brown, with two moderate retromargin teeth and two promargin teeth, the distal larger and proximal smaller than the retromargin teeth. No clear denticle present.

Coxae all light yellow-brown. Trochanter IV notch moderately small.

All femora yellow-brown with some black and white hairs. Rest of legs I and II light yellow-brown; rest of legs III and IV yellow-brown. Tibia I ventral spination: 3–2, strong and fairly long. Legs fairly heavily hirsute.

External epigynum with two small, widely separated, round openings (Fig. 97). Internal structure with rounded sper-

mathecae narrowing slightly to wide posterior necks (Fig. 96).

Diagnosis. *Castianeira occidens* differs from other *descripta* group species in the longitudinal white band on its carapace and its somewhat longer, thinner spermathecal necks (Fig. 96).

Remarks. This species is very closely related to *C. descripta.*

Natural history. This species has been collected in dryish grass and mesquite in southeastern Arizona, as well as in the forested mountains up to 8000 feet. A white disclike egg case contained 16 first instar spiderlings.

C. occidens is a fast running spider and possibly a mutillid wasp mimic.

Distribution. Southwestern U.S. and N. W. Mexico (Map 5).

Castianeira walsinghami (O. P.-Cambridge) Figures 92–95, 122. Map 5.

Agroeca walsinghami O. P.-Cambridge, 1874, Proc. Zool. Soc. London 1874:416, ♂, from Oregon; in the Oxford Museum, examined.
Castaneira walsinghami: Simon, 1897, Histoire Naturelle des Araignées, II (1):167.
Castianeira walsinghami: Banks, 1910, Bull. U.S. Nat. Mus. 72:11.

MALE

Measurements. Based on holotype and 2 males, holotype listed first, range of all follows: carapace length 3.05 mm, 3.05–3.40 mm; carapace width 2.05 mm, 2.05–2.35 mm; carapace index 68, 68–70; sternum length 1.25 mm, 1.25–1.50 mm; sternum width 1.10 mm, 1.10–1.25 mm; sternum index 90, 82–90.

Femur IV length 2.50 mm, 2.50–2.70 mm; femur IV width 0.60 mm, 0.60–0.75 mm; leg thickness index 25, 25–27; leg length index 82, 80–82.

Abdomen length 3.30 mm, 3.30–3.65 mm; abdomen width 1.75 mm, 1.60–2.05 mm; abdomen index 53, 47–56.

Embolus length 0.16 mm, 0.16 mm; bulb length 1.04 mm, 1.04–1.09 mm; male genital index 16, 15–16.

Description. Lightly pigmented specimen. Light orange-brown carapace with black and white plumose hairs—white hairs along center, longer in the cephalic region. Eyes moderately small, equal, and bordered in black. Carapace narrows in head region (cephalic width index 51–52) and is truncated smoothly anteriorly. Thoracic groove moderately strong.

Abdomen a long oval with an almost full dorsal sclerite with white hairs at anterior end and mostly orange-red plumose hairs on the rest, with a longitudinal band of darker hairs down anterior part of midline (many hairs rubbed off). A pair of light pigment spots just anterior to middle and almost meeting to produce a wide horizontal band. Light yellow-brown epigastric and almost full ventral sclerites. A long white spot on each side of abdomen. First pair of abdominal setae very thin, second pair thin.

Sternum orange with moderately dense, thin setae.

Chelicerae orange-brown with two moderate retromargin teeth and two promargin teeth, the distal longer and the proximal smaller than the retromargin teeth. No distinct denticle present.

Coxae all light yellow. Trochanter IV notch moderate.

Femora all light yellow. Rest of legs I and II light yellow; rest of legs III and IV light yellow-brown, with leg IV slightly darker, especially metatarsus IV. Legs moderately hirsute. Tibia I ventral spination: 2–2, moderate.

Pedipalp with a short, blunt apophysis. Tarsus with a globose genital bulb drawn out into a long neck with a moderately long, thin, and straight embolus (Figs. 94, 95).

FEMALE

Measurements. Based on 4 females: carapace length 3.65–4.05 mm; carapace width 2.45–2.75 mm; carapace index 67–69; sternum length 1.65–1.75 mm; sternum width 1.40–1.55 mm; sternum index 84–89.

Femur IV length 2.95–3.20 mm; femur IV width 0.80–0.85 mm; leg thickness index 26–27; leg length index 79–82.

Abdomen length 3.75–5.60 mm; abdomen width 2.30–4.10 mm; abdomen index 61–76; dorsal sclerite length 0.55–0.95 mm; dorsal sclerite width 0.95–1.20 mm; dorsal sclerite index 124–206.

Description. Light orange-brown carapace with some black and white plumose hairs. Eyes moderately small, equal, and bordered in black. Carapace narrows in head region (cephalic width index 57–60) and is smoothly truncated anteriorly. Thoracic groove moderate.

Abdomen oval, with a small, anterior, orange dorsal sclerite and a hair pattern (many hairs rubbed off) of white hairs at anterior end and horizontal bands of orange plumose hair surrounded by brown-black hairs, with a large band (split in middle) just anterior to middle, followed and connected to two bands (fused in middle) and a posterior, longitudinal bar. Light yellow-brown epigastric sclerite. First pair of abdominal setae very thin, second pair thin.

Sternum yellow-brown with moderately dense, thin setae.

Chelicerae light orange-brown, with two moderate retromargin teeth and two promargin teeth, the distal longer and the proximal smaller than the retromargin teeth. No distinct denticle present.

Coxae all light yellow-brown. Trochanter IV notch moderate.

Femora all yellow. Rest of legs I and II light yellow; rest of legs III and IV light yellow-brown, with leg IV slightly darker, especially metatarsus IV. Legs moderately hirsute. Tibia I ventral spination: 3–2, long and strong.

External epigynum with two small circular openings (Fig. 93). Internal structure with two rounded, sac-like spermathecae with wide posterior necks (Fig. 92).

Diagnosis. Castianeira walsinghami differs from other *descripta* group species in its distinctive abdominal pattern.

Remarks. This is closely related to the preceding two species.

Natural history. C. walsinghami is found under stones in coniferous forest (Worley, 1932).

Distribution. Oregon and Washington (Map 5).

Records. Oregon. Washington. San Juan Co.

Castianeira crucigera (Hentz)

Figures 62–65, 86, 87. Map 5.

Herpyllus cruciger Hentz, 1847, Boston J. Nat. Hist. Soc. 5:458, pl. 24, fig. 11, ♀, from North Carolina; lost.

Castianeira crucigera: Chamberlin and Ivie, 1944, Bull. Univ. Utah 35(9) Biol. Ser. 8(5):180, fig. 20 (Abbot 458), ♂.

MALE

Measurements. Based on 3 males: carapace length 3.10–3.20 mm; carapace width 2.05–2.10 mm; carapace index 65–67; sternum length 1.40–1.45 mm; sternum width 1.10–1.20 mm; sternum index 78–84.

Femur IV length 2.45–2.60 mm; femur IV width 0.70–0.75 mm; leg thickness index 27–30; leg length index 78–82.

Abdomen length 3.40–3.60 mm; abdomen width 1.65–1.85 mm; abdomen index 48–52.

Embolus length 0.15–0.18 mm; bulb length 0.99–1.03 mm; male genital index 15–18.

Description. Carapace dark red-brown, covered with dense, short, white hairs. Carapace moderately narrow in head region (cephalic width index 54–60) and smoothly but distinctly truncated anteriorly. Eyes small and approximately equal. Thoracic groove moderately strong and short.

Abdomen oval, with four-fifths full, dark red-brown, dorsal sclerite and a black and white hair pattern—a wide longitudinal white hair band narrowing posteriorly, with two median dark spots in the band, one a quarter way from anterior end and a smaller one halfway back (Fig. 86). An

anterior white hair spot on each side of abdomen. Ventral abdomen with a wide, rectangular, dark red-brown sclerite narrowing posteriorly and extending about two thirds of the way from epigastric furrow to spinnerets. No inframammilliary sclerite present. Both pairs of abdominal setae thin.

Sternum red-brown and covered with fairly dense, short, white hair, as well as the typical long setae. Pedicel short.

Chelicerae deep red-brown, with two moderate retromargin teeth (the distal slightly longer) and two promargin teeth—the distal somewhat larger and the proximal much smaller than the retromargin teeth, with a very small, but clear, denticle just distal to the larger promargin tooth.

Coxae all red-brown but lighter at distal tips. Rest of legs I and II yellow-white; rest of leg III yellow-brown, but with longitudinal stripes of brown and yellow on patella-tibia, and tarsus lighter; rest of leg IV red-brown, with patella-tibia also striped as in leg III, and tarsus yellow-brown. Legs quite heavily hirsute. Tibia I ventral spination: 2–2, moderately small.

Pedipalp with low rounded apophysis. Tarsus with a globose genital bulb drawn out into a long neck with a straight, moderately thin, and long embolus coming to a point (Figs. 64, 65).

FEMALE

Measurements. Based on 2 females: carapace length 2.75–3.70 mm; carapace width 1.90–2.40 mm; carapace index 65–69; sternum length 1.20–1.60 mm; sternum width 1.05–1.30 mm; sternum index 82–87.

Femur IV length 2.30–2.85 mm; femur IV width 0.65–0.85 mm; leg thickness index 28–30; leg length index 77–85.

Abdomen length 3.30–4.30 mm; abdomen width 1.90–2.45 mm; abdomen index 57; dorsal sclerite width 0.95–1.05 mm.

Description. Carapace red-brown, covered with white hairs, longer on head. Eyes fairly small, about equal, and ocular region black. Carapace narrower in head region (cephalic width index 53–55) and smoothly truncated anteriorly. Thoracic groove moderately strong and short.

Abdomen oval, with a small, red-brown, anterior dorsal sclerite and a black and white hair pattern—basically a complete, longitudinal, median white hair band narrowing posteriorly and spreading laterally in three bands, two at anterior end and one median, and two dark spots within the longitudinal band, a large one anterior to median band, and one at the level of the median band (Fig. 87). Wide white hair bands on both sides of abdomen. Epigastric sclerite red-brown. Ventral abdomen with four parallel, beaded stripes, two from ends of epigastric furrow and two more median, continuing posteriorly to spiracular furrow. Both pairs of abdominal setae very thin.

Sternum red-brown, with long, thin setae and shorter hairlike setae.

Chelicerae red-brown, with two moderate retromargin teeth (the distal slightly larger) and two promargin teeth—the distal somewhat larger and the proximal smaller than the retromargin teeth, with a small, but clear, denticle just distal to the larger promargin tooth.

Coxae all light yellow-brown. Trochanter IV notch moderate.

Femora reddish brown. Rest of legs I and II deep yellow-brown; rest of legs III and IV red-brown, lightening at distal ends of femora, patellae, and tibiae. Legs quite heavily hirsute, with black and white hairs. Tibia I ventral spination: 3–2, moderately long and strong.

External epigynum with two small, round openings widely separated (Fig. 63). Internal structure with moderately globose spermathecae narrowing somewhat posteriorly (Fig. 62).

Diagnosis. Castianeira crucigera differs from all other *Castianeira* in its abdominal pattern.

Remarks. This striking species is rediscovered and redescribed here. Chamberlin and Ivie (1944) note the illustration of this

species by Abbot (1792, No. 458), but the dark spots on the head of Abbot's drawing are not present in the species or in Hentz's (1847) more accurate drawing.

Castianeira crucigera in its female genitalia is somewhat intermediate in structure between the *descripta* group and the *longipalpus* group, but the small openings and thick spermatheceal necks place it with the former group.

Natural history. Castianeira crucigera is found in the non-forest maritime communities of North Carolina (Barnes, 1953a, where *C. vulnerea* is actually *C. crucigera*) and throughout the South. Hentz (1847) reported that this species moves "with great celerity, and hides under stones, etc."

Distribution. Southeastern U.S. (Map 5).

Records. Arkansas. Conway Co. *North Carolina.* Cartaret Co. *Virginia.* Fairfax Co.

Castianeira vulnerea Gertsch

Figures 46–49, 81. Map 5.

Castianeira vulnerea Gertsch, 1942, Amer. Mus. Novit. No. 1195:7, figs. 22–23, ♂, ♀. Male holotype from Coney Island, New York; in the American Museum of Natural History, examined.

MALE

Measurements. Based on one male holotype: carapace length 2.10 mm; carapace width 1.50 mm; carapace index 72; sternum length 0.95 mm; sternum width 0.85 mm; sternum index 87.

Femur IV length 1.80 mm; femur IV width 0.45 mm; leg thickness index 25; leg length index 86.

Abdomen length 2.45 mm; abdomen width 1.25 mm; abdomen index 51.

Embolus length 0.11 mm; bulb length 0.77 mm; male genital index 15.

Description. Carapace deep orange-brown with white hairs. Eyes small, about equal, and bordered in black. Carapace narrower in head region (cephalic width index 57) and smoothly truncated anteriorly. Thoracic groove moderately strong.

Abdomen elongated oval with an almost full, orange dorsal sclerite covered with some partially rubbed off bands of white hair. Sides of abdomen with three white hair spots joined into a lateral-ventral white hair stripe. Ventral abdomen with a dark yellow rectangular sclerite about two-thirds of the way from epigastric furrow to spiracular furrow. No inframammilliary sclerite present. Epigastric sclerite red-brown. Anterior abdominal setae thin, posterior pair stouter.

Sternum red-brown with sparse, thin setae. Pedicel very small.

Chelicerae deep orange-brown, with two moderate retromargin teeth (the distal slightly longer) and two promargin teeth, the distal one larger and the proximal one slightly smaller than the retromargin teeth; a very small denticle just distal and median to the distal promargin tooth.

Coxae all light yellow-brown. Trochanter IV notch moderate.

Femora red-brown; rest of legs I and II deep yellow; rest of leg III orange-brown; rest of leg IV red-brown, slightly lighter at the distal ends of the patella and tibia. Legs moderately hirsute. Tibia I ventral spination: 2–2, moderate, proximal retrolateral spine smaller.

Pedipalp with a small, blunt, tibial apophysis. Tarsus with a globose genital bulb drawn out into a long neck with a fairly short, straight, and fairly thin embolus (Figs. 48, 49).

FEMALE

Measurements. Based on one female (paratype): carapace length 2.60 mm; carapace width 1.80 mm; carapace index 69; sternum length 1.20 mm; sternum width 1.05 mm; sternum index 89.

Femur IV length 2.20 mm; femur IV width 0.60 mm; leg thickness index 28; leg length index 85.

Abdomen length 3.25 mm; abdomen width 2.05 mm; abdomen index 62; dorsal sclerite width 0.80 mm.

Description. Carapace orange-brown, with white hairs. Eyes small, about equal, and bordered in black. Carapace narrower in head region (cephalic width index 55) and smoothly truncated anteriorly. Thoracic groove moderately strong.

Abdomen oval, with a small orange-brown sclerite and a white and brown-black dorsal hair pattern—three horizontal white hair bands along median line, first and second joined at median, and not continuing to sides, then a complete horizontal band of white hairs, followed by a longitudinal band of white hairs (not continuous anteriorly) to the spinnerets (Fig. 81). Abdomen with a white hair stripe and three spots along its dorsal side. Ventrum with brown hairs. No inframammilliary sclerite. Anterior abdominal setae hairlike, posterior pair very thin.

Sternum orange-brown, with long, thin setae. Pedicel very small.

Chelicerae orange, with two moderate retromargin teeth (the distal slightly longer) and two promargin teeth, the distal one larger and the proximal one slightly smaller than the retromargin teeth; a very small denticle just distal and median to the distal promargin tooth.

Coxae all light yellow. Trochanter IV notch moderate.

Femora light red-brown; rest of legs I and II dark yellow; of leg III yellow-brown; leg IV light red-brown, lighter at distal ends of patella and tibia. Legs moderately hirsute. Tibia I ventral spination: 3–2, moderate, proximal prolateral spine much smaller.

External epigynum with two fairly small, round openings (Fig. 46). Internal structure with rounded spermathecae and narrowed, slightly folded necks (Fig. 47).

Diagnosis. Castianeira vulnerea differs from other *longipalpus* group species in its abdominal pattern and internal epigynum; the spermathecal necks are fairly thick and turned inward (Fig. 47).

Remarks. This species is closely related to *Castianeira crucigera*, the genitalia very similar in both the males (Figs. 48, 64) and the females (Figs. 47, 62). The abdominal patterns are quite different, but the scarcity of available *C. vulnerea* prevents a study of the possible north to south variation. The female genitalia of *C. vulnerea* more closely resemble those of *C. descripta* than do those of *C. crucigera.*

Natural history. Nothing is known of the habits of this species.

Distribution. New York (Map 5).

Records. New Jersey. Essex Co. *New York.* Kings Co.

THE *GERTSCHI* GROUP

Castianeira gertschi Kaston

Figures 104–107, 120. Map 7a.

Castianeira aurata: Emerton, 1913, Bull. Amer. Mus. Nat. Hist. 32:258, pl. 48, figs. 8–8b, ♂, ♀. (Not *Herpyllus? auratus* Hentz.)

Castianeira gertschi Kaston, 1945, Amer. Mus. Novit. No. 1290:6, figs. 27–29, ♂, ♀. Male holotype from Indian Neck, Connecticut; in the American Museum of Natural History, examined.

MALE

Measurements. Based on holotype and 6 males, holotype listed first, range of all follows: carapace length 2.50 mm, 2.00–2.50 mm; carapace width 1.60 mm, 1.20–1.60 mm; carapace index 64, 61–64; sternum length 1.20 mm, 0.95–1.20 mm; sternum width 0.75 mm, 0.70–0.85 mm; sternum index 62, 62–77.

Femur IV length 2.05 mm, 1.65–2.15 mm; femur IV width 0.50 mm, 0.35–0.50 mm; leg thickness index 23, 21–23; leg length index 83, 82–90.

Abdomen length 2.75 mm, 2.15–2.75 mm; abdomen width 1.20 mm, 1.00–1.20 mm; abdomen index 44, 39–47.

Embolus length 0.11 mm, 0.10–0.11 mm; bulb length 0.86 mm, 0.75–0.86 mm; male genital index 13, 12–13.

Description. Carapace yellow-orange and hairless. Eyes fairly small, equal, and bordered in black. Carapace narrow in head region (cephalic width index 50–55)

and smoothly truncated anteriorly. Thoracic groove moderate.

Abdomen an elongated oval, with a complete dorsal sclerite yellow at anterior end and gradually darkening to a dark brown at posterior end and crossed by three lighter bands (reinforced with white hairs), the most posterior being median and split in the middle (Fig. 120). Light red-brown epigastric sclerite. Elongated, rectangular, yellow ventral sclerite from epigastric furrow to a small inframammilliary sclerite. Anterior abdominal setae very thin, posterior pair considerably stouter.

Sternum yellow, with very sparse, thin setae. Pedicel very small.

Chelicerae dark yellow, with two moderate retromargin teeth and two promargin teeth, the distal one much larger and the proximal one smaller than the retromargin teeth; with a small but clear denticle just distal and medial to the larger promargin tooth.

Coxae deep yellow. Trochanter IV notch moderate.

Femora all yellow-orange. Rest of legs I and II light yellow; of leg III deep yellow; leg IV patella yellow-orange, tibia red-brown, metatarsus darker red-brown, tarsus orange-brown. Legs moderately hirsute. Tibia I ventral spination: 2–2.

Pedipalp with moderate, pointed, tibial apophysis. Tarsus with a globose genital bulb drawn out into a long neck with a short, fairly thin embolus with a clear twist at the tip (Figs. 106, 107).

FEMALE

Measurements. Based on 5 females: carapace length 2.35–2.85 mm; carapace width 1.40–1.80 mm; carapace index 59–63; sternum length 1.05–1.30 mm; sternum width 0.80–0.95 mm; sternum index 68–76.

Femur IV length 2.05–2.25 mm; femur IV width 0.40–0.60 mm; leg thickness index 20–26; leg length index 83–88.

Abdomen length 2.80–3.85 mm; abdomen width 1.15–2.50 mm; abdomen index 41–68; dorsal sclerite length 0.55–0.65 mm; dorsal sclerite width 0.55–0.70 mm; dorsal sclerite index 85–117.

Description. Carapace deep yellow-orange and hairless. Eyes fairly small, equal, and bordered in black. Carapace narrow in head region (cephalic width index 55–60) and smoothly truncated anteriorly. Thoracic groove moderately strong.

Abdomen oval with a moderately small, yellow, anterior dorsal sclerite; abdomen darkening to dark brown at posterior end. Epigastric sclerite yellow-orange. Anterior abdominal setae long and very thin; posterior pair shorter and stouter. (Vague horizontal stripes on abdomen.)

Sternum yellow, with very sparse, long, thin setae.

Chelicerae dark yellow, with two moderate retromargin teeth and two promargin teeth, the distal one much larger and the proximal one smaller than the retromargin teeth; with a small but clear denticle just distal and medial to the larger promargin tooth.

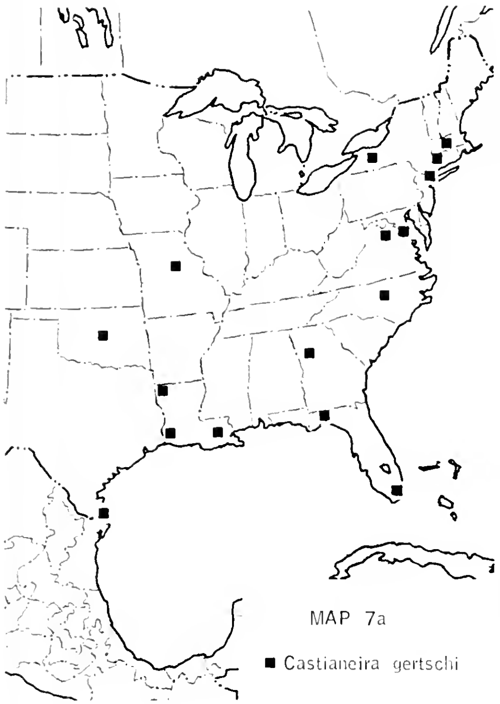
Coxae all deep yellow. Trochanter IV notch moderate.

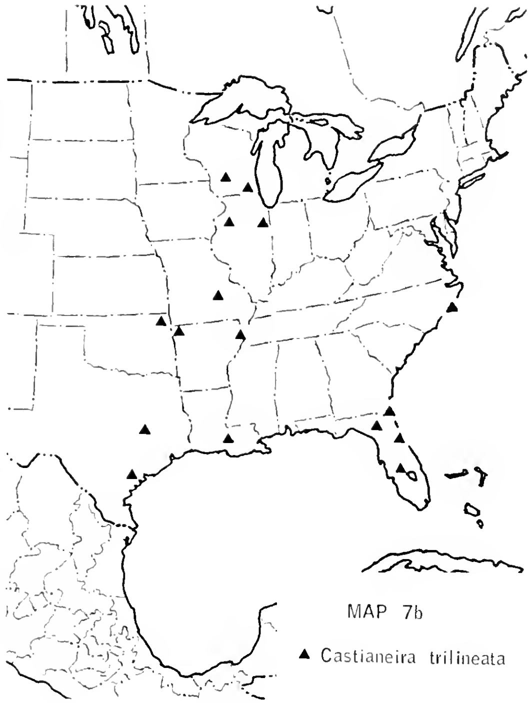
Femora I and II deep yellow, rest of legs I and II light yellow. Femur and patella-tibia III deep yellow, rest of leg III yellow-brown; femur and patella-tibia IV yellow-orange (darkening to red-brown at distal end of tibia), metatarsus and tarsus deep red-brown. Legs moderately hirsute. Tibia I ventral spination: 2–2, strong.

External epigynum with two flared openings (Fig. 105). Internal structure with globose spermathecae having narrow posterior necks (Fig. 104).

Diagnosis. This moderately small spider differs from other *Castianeira* in its abdomen, which darkens posteriorly from yellow to dark brown, often having three horizontal stripes (Fig. 120). Genitalic differences distinguish it from the larger *Castianeira trilineata.*

Remarks. *Castianeira gertschi* is the





name given to a species previously known as *Castianeira aurata* (Hentz) (e. g. described by Emerton in 1913). Kaston (1945) noted that *Herpyllus auratus* Hentz, on which the old name was based, was actually a *Micaria*; therefore a new name was in order.

Natural history. Nothing is known of the habits of this species.

Distribution. Southern New England to the southeastern U.S. (Map 7a).

THE *TRILINEATA* GROUP

Castianeira trilineata (Hentz)

Figures 108–110, 119. Map 7b.

Herpyllus trilineatus Hentz, 1847, Boston J. Nat. Hist. Soc. 5:460, pl. 24, fig. 18, ♀, from Alabama; lost.

Thargalia trilineata: Marx, 1889, Proc. U.S. Nat. Mus. 12:514.

Castianeira trilineata: Banks, 1910, Bull. U.S. Nat. Mus. 72:11.

Castianeira stupkai Barrows, 1940, J. Ohio Sci. 40(3):137, figs. 10, 10b, 10c, ♂, ♀. Male holotype from Gatlinburg, Tennessee; in the Ohio State University Museum, examined. NEW SYNONYMY.

Castianeira trilineata: Kaston, 1948, Connecticut Geol. and Nat. Hist. Surv. Bull. 70:397, figs. 1423, 2123, ♂, ♀.

MALE

Measurements. Based on 10 males: carapace length 2.50–3.05 mm; carapace width 1.50–1.85 mm; carapace index 59–62; sternum length 1.10–1.40 mm; sternum width 0.80–1.05 mm; sternum index 73–81.

Femur IV length 1.90–2.55 mm; femur IV width 0.35–0.50 mm; leg thickness index 18–22; leg length index 75–89.

Abdomen length 2.75–3.50 mm; abdomen width 1.20–1.75 mm; abdomen index 44–55.

Bulb length 0.95–1.10 mm.

Description. Carapace orange-brown and hairless. Eyes moderate and equal. Carapace narrower in head region (cephalic

width index 48–53) and rounded anteriorly. Thoracic groove fairly weak.

Abdomen a slightly pear-shaped oval, widening posteriorly and covered by a full, red-brown dorsal sclerite with a thin horizontal light yellow band across midline and some horizontal yellow-brown abbreviated stripes at anterior end (Fig. 119). Epigastric sclerite red-brown. Rectangular, red-brown ventral sclerite from epigastric furrow to a small brown inframammilliary sclerite. First pair of abdominal setae long and hair-like, second pair stout and moderately thick.

Sternum orange-brown, with very sparse, thin setae. Pedicel small.

Chelicerae light orange-brown, with two moderately small retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth; with a minute denticle just medial and distal to the larger promargin tooth.

Coxa I brown, coxae II–IV yellow-white. Trochanter IV notch moderate.

Femora I red-brown, II and III striped with red-brown lateral sides and yellow dorsal and ventral sides, and IV with red-brown lateral sides, and a medial dorsal stripe; rest of I and II yellow-white with distal ends of metatarsi brown; rest of III yellow with patella-tibia and metatarsus striped like femur; rest of IV with striped patella-tibia, brown metatarsus, and yellow tarsus. Legs lightly hirsute. Tibia I ventral spination: 3–2, small.

Pedipalp with a small tibial apophysis. Tarsus with a globose genital bulb drawn into a short neck with a complex twisted embolus and conductor end (Fig. 110). The basal portion of the lateral side of the cymbium bears a heavy spine.

FEMALE

Measurements. Based on 10 females: carapace length 2.70–3.65 mm; carapace width 1.65–2.40 mm; carapace index 59–64; sternum length 1.20–1.65 mm; sternum width 0.95–1.30 mm; sternum index 77–82.

Femur IV length 2.20–3.25 mm; femur IV width 0.40–0.65 mm; leg thickness index 14–23; leg length index 80–92.

Abdomen length 3.20–4.50 mm; abdomen width 1.95–3.05 mm; abdomen index 54–70; dorsal sclerite length 0.70–1.10 mm; dorsal sclerite width 0.75–0.95 mm; dorsal sclerite index 88–138.

Description. Carapace light yellowish-brown (head region slightly darker) and hairless. Eyes moderate, bordered in black, and equal. Carapace narrower in head region (cephalic width index 54–58) and smoothly truncated anteriorly. Thoracic groove fairly weak.

Abdomen oval, with a moderate, brown dorsal sclerite, dark black-brown with three thin horizontal bands—two thin yellow-white bands, one through the sclerite, one at middle of abdomen, and one wider, dark yellow-brown band near the posterior end. Epigastric sclerite light brown on sides, cream colored along midline. Ventrum dark brown with four longitudinal, light, beaded stripes from epigastric furrow to a moderately small, brown inframammilliary sclerite. First pair of abdominal setae hair-like, second pair thin.

Sternum yellow-white with sparse, thin setae. Pedicel very small.

Chelicerae light yellow-brown, with two moderately small retromargin teeth (the distal one slightly larger) and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth; with a minute denticle just medial and distal to the larger promargin tooth.

Coxae all light yellow. Trochanter IV notch very shallow.

Femora I and II with brown lateral sides, femora III and IV with very light brown lateral sides; rest of legs I and II yellow-white, of leg III light yellow, of leg IV yellow, with darker tibia and metatarsus. Tibia I ventral spination: 3–3, moderate spines. Legs lightly hirsute.

External epigyum with two wide, flared openings (Fig. 109). Internally with rounded spermathecae and narrow, slightly sinuous posterior necks (Fig. 108).

Diagnosis. The males of *Castianeira trilineata* differ from all other *Castianeira* in their short, twisted embolus (Fig. 110). The females have a hairless carapace, flared epigynal openings, and a distinctive abdominal pattern of three horizontal light bands.

Remarks. There is a great deal of color variation in *C. trilineata*, with a very dark brown form occurring in the middle of Florida and a yellow to orange form occuring elsewhere (northern Florida, Missouri, Illinois, etc.).

Natural history. Castianeira trilineata is found in sandy places, under dead leaves on Long Island (Banks, 1895), in nonforest maritime communities of North Carolina (Barnes, 1953b), on the ground stratum of river-terrace forest of western Tennessee (Gibson, 1947), in black oak forest in the Chicago area dunes (Lowrie, 1948, Fitch, 1963), and in an Andropogon field of eastern Tennessee (Barrows, 1940).

Gibson (1947) reports this species hatching in middle August and maturing in late July, the spiders overwintering in the egg case as eggs or very young. Fitch (1963) notes that "in size, coloration and behavior it resembles the carpenter ant, *Camponotus castaneus*, which is common in the same habitat." One specimen was collected with a worker of *Formica pallidefulva* in Missouri.

Distribution. Eastern U.S. (Map 7b).

The *cingulata* Group

Castianeira cingulata (C. L. Koch)

Frontispiece. Figures 100–103, 116–118. Map 7c.

Corinna cingulata C. L. Koch, 1842, Die Arachniden 9:22, fig. 706, ♀, from Pennsylvania; lost.

Herpyllus zonarius Hentz, 1847, Boston J. Nat. Hist. Soc. 5:460, pl. 24, fig. 17, ♀, from Alabama; lost.

Sparassus cingulata: Walckenaer, 1847, Histoire Naturelle des Insectes Aptères 4:562.

Thargalia cingulata: Karsch, 1880, Z. Ges. Nat. 53:376. Marx, 1889, Proc. U.S. Nat. Mus. 12: 513. Marx, 1892, Proc. Entomol. Soc. Washington 2(2):155.

Liocranum zonarium: Marx, 1883, Araneina, *in* Howard, L. O., A List of the Invertebrate Fauna of South Carolina, Charleston, p. 23.

Castianeira bivittata Keyserling, 1887, Verhandl. Zool. Bot. Ges. Wien 37:442, pl. 6, fig. 16, ♀, from Cambridge, Massachusetts; in the Museum of Comparative Zoology, examined.

Geotrecha bivittata: Emerton, 1889, Trans. Connecticut Acad. Sci. 8(9):169, pl. 3, fig. 3, ♂, ♀. Emerton, 1902, The Common Spiders of the United States, Boston, p. 8, fig. 23–24.

Thargalia zonaria: Marx, 1889, Proc. U.S. Nat. Mus. 12:514.

Thargalia bivittata: Marx, 1889, Proc. U.S. Nat. Mus. 12:513.

Castaneira cingulata: Simon, 1897, Histoire Naturelle des Araignées, II, fasc. 1:172. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist. 29: 452.

Thargalia canadensis Banks, 1897, Canadian Entomol. 29:194, ♀, from Ottawa, Canada; in the Museum of Comparative Zoology, examined. (First synonymized by Emerton, 1920, Trans. Roy. Canadian Inst. 12:332 as *Micaria cingulata.*)

Castianeira cingulata: Banks, 1910, Catalogue of Nearctic Spiders, Bull. U.S. Nat. Mus. 72:11 (= *bivittata* = *zonaraia*). Chickering, 1939, Pap. Michigan Acad. Sci. 24(2):57, figs. 17–19, ♂, ♀. Kaston, 1948, Connecticut Geol, and Nat. Hist. Surv. Bull. 70:394, figs. 1401, 1408, 1424–1425, ♂, ♀.

MALE

Measurements. Based on 10 males: carapace length 2.80–3.40 mm; carapace width 1.70–2.05 mm; carapace index 59–63; sternum length 1.15–1.45 mm; sternum width 0.95–1.10 mm; sternum index 75–81.

Femur IV length 1.95–2.60 mm; femur IV width 0.45–0.60 mm; leg thickness index 22–25; leg length index 67–81.

Embolus length 0.22–0.26 mm; bulb length 1.30–1.57 mm; male genital index 16–18.

Description. Carapace rounded anteriorly (Fig. 116) (cephalic width index 48–49) and very dark maroon, with fairly long, simple, white hairs on cephalic region and

some light hairs covering triangle made by posterior truncation of carapace and thoracic groove. Eyes moderately small and equal. Thoracic groove moderate.

Abdomen oval, widening posteriorly, and covered with a dark maroon dorsal sclerite and two narrow, horizontal, lighter pigmented stripes, the anterior one at one fourth and the posterior one at one half the length of the abdomen (Fig. 117). Both bands reinforced by long, simple, white hairs. Rest of abdomen covered by dark hairs. Epigastric sclerite red-brown. Ventral sclerite rectangular and red-brown, running from epigastric furrow posteriorly and ending in semicircle around an orange-brown inframammilliary sclerite. Anterior pair of dorsal abdominal setae long and very thin, posterior pair shorter and stouter.

Sternum red-brown, with sparse, very long setae. Pedicel short.

Chelicerae red-brown, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth. A very small denticle distal and medial to larger promargin tooth.

Coxa I light brown, coxae II, III, and IV yellow-white. Trochanter IV with a shallow notch.

Femora of all legs striped—both lateral sides and dorsal stripe dark brown, rest of femora dark yellow or orange. The resulting light stripes reinforced with white hairs on femora II, III, and IV. Tibiae III and IV similarly striped, and sides of patellae III and IV dark brown; metatarsus IV dark brown; rest of legs I and II yellow-white, of leg III dark yellow, of leg IV orange. Legs lightly hirsute with moderate spination. Tibia I ventral spination: 3–2, small.

Pedipalp with a negligible tibial apophysis. Tarsus with globose genital bulb drawn out into long neck with a club-shaped sclerotized embolus having a very strongly spiraled tip (Figs. 102, 103).

FEMALE

Measurements. Based on 11 females: carapace length 3.10–3.75 mm; carapace width 2.00–2.40 mm; carapace index 62–65; sternum length 1.40–1.65 mm; sternum width 1.10–1.30 mm; sternum index 74–80.

Femur IV length 2.40–2.95 mm; femur IV width 0.60–0.70 mm; leg thickness index 23–25; leg length index 75–83.

Description. Carapace maroon, with sparse white hairs in cephalic region. Carapace narrow in head region (cephalic width index 54–60) and smoothly truncated anteriorly. Ocular region darker. Eyes moderate and equal. Thoracic groove moderate.

Abdomen rounded oval, with a small, red-brown dorsal sclerite; two thin, light pigmented, horizontal bands, one crossing the dorsal sclerite, the other about one fourth abdominal length from anterior end. White hairs reinforce pigment bands and dark hairs cover grey basal color of rest of abdomen (Fig. 115). Epigastric sclerite red-brown. Two light pigmented lines of beaded stripes running parallel from sides of epigastric furrow to area on sides of posterior spiracular furrow. Anterior pair of dorsal abdominal setae long and hairlike, posterior pair shorter and fairly thick (arising from the dorsal scutum).

Sternum red-brown, shield-shaped, with long, thin setae. Pedicel fairly short.

Chelicerae dark brown, with two moderately large retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth. A very small denticle distal and medial to the larger promargin tooth.

Coxa I brown, coxae II and III yellow, and coxa IV dark yellow. Trochanter IV with shallow notch.

Femora of all legs striped—both lateral sides and dorsal stripes dark brown, rest of femora yellow. Resulting dorsal yellow stripes reinforced with white hairs on femora III and IV. Tibiae III and IV simi-

larly striped (the former weakly); metatarsus IV dark brown; rest of legs I and II yellow, rest of leg III orange, and of leg IV orange-brown. Legs lightly hirsute, with moderate spination. Tibia I ventral spination: 3–2, moderately thin and long.

External epigynum with widely flared openings (Fig. 101). Internal structure with a pair of saclike, rectangular, heavily sclerotized, and heavily reticulated spermathecae (Fig. 100).

Diagnosis. *Castianeira cingulata* differs from all other *Castianeira* in its distinct genitalia, abdomen with two thin horizontal bands, and strongly striped legs.

Remarks. A form of *C. cingulata* with a bicolored carapace (a dark brown cephalic region and an orange or yellow thoracic region) is found in northern Wisconsin, Minnesota, South Dakota, and Ontario (see Map 7c). Both forms occur together in Minnesota, and near one another in South Dakota. These two phenotypes may represent another example of genetic polymorphism in spiders.

Natural history. *Castianeira cingulata* is found in forest litter, beneath logs and stones and among leaves on the ground in Michigan (Chickering, 1939), under sandstone, under elm logs, in elm shrubbery in the prairies and forests of eastern Nebraska (Worley and Pickwell, 1931), in ground stratum of elm-maple forest in Illinois (Weese, 1924), in black oak and beech maple forest of the Chicago area dunes (Lowrie, 1948), on the ground among leaf mold in Ontario (Kurata, 1939), and in oak-hickory woodland in Kansas (Fitch, 1963).

C. cingulata hibernates in immature or adult form (Elliot, 1930), and adult females have been collected in eastern Massachusetts in December. Jones (1941) observed mature and immature specimens in the winter and one hibernating in an empty acorn shell. Kaston (1948) reports finding females in winter, spring, and summer, but males only in July and August.

Of four egg cases collected by Kaston (1948), one had 22 eggs, two had 24 eggs each, and one had 30 eggs.

Montgomery (1903) described the construction of the egg case, noting that after finishing the spinning, the spider "covered the surface . . . with small particles of dirt."

Truman (1942) reported *C. cingulata* running at night "in company with the large carpenter ants, which it closely resembles both in appearance and in action."

Distribution. Eastern and midwestern U.S. and Canada (Map 7c).

THE *DUGESII* GROUP

Characteristics. Moderately small (male carapace length 1.60–2.15 mm; female carapace length 1.90–2.85 mm), with a carapace index 61–69. Whole body almost hairless, with some light hairs on abdomen. Spermathecae with globose anterior ends and moderately thin posterior crooked necks. External epigynum with flared openings. Leg thickness index 18–26. Eyes approximately equal.

Remarks. This group is restricted to the dry regions in southwestern U.S. and northwestern Mexico and is characterized by its hairlessness and distinctive male genitalia.

Castianeira dugesii (Becker)

Figures 127, 128. Map 8.

Micariaulax dugesii Becker, 1879, Ann. Soc. Entomol. Belgium, 22:83, pl. 2, fig. 9, 10, ♂, from Guanajuato, Mexico; in the Brussels Museum, examined.

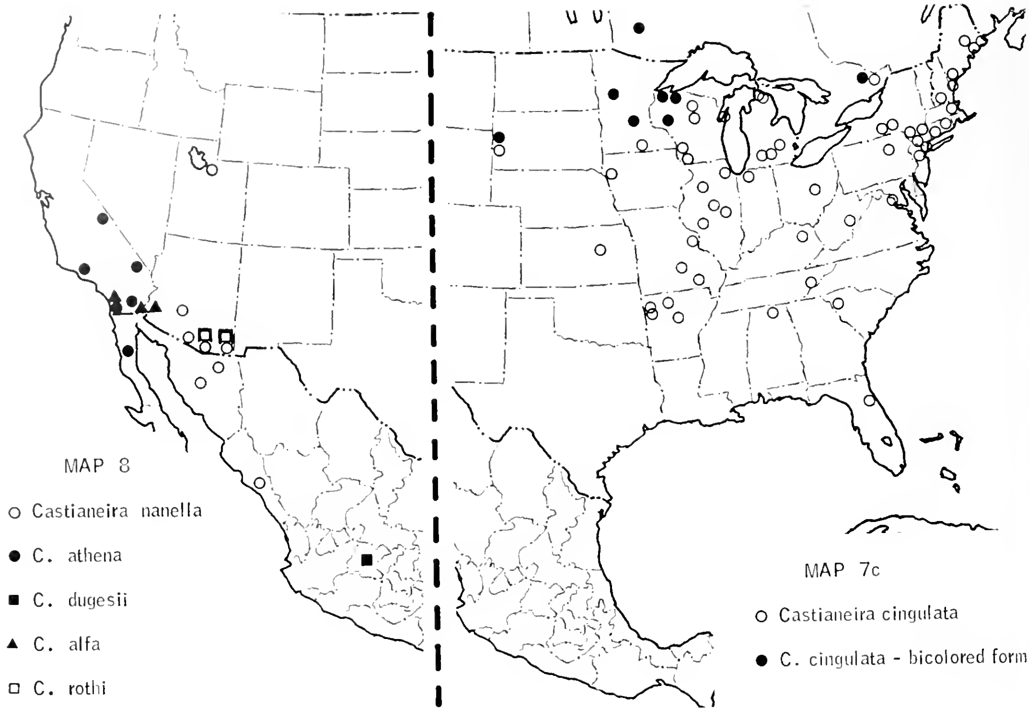
Castaneira dugesii: Simon, 1897, Histoire Naturelle des Araignées 2(1):167.

Castianeira dugesii: F. P.-Cambridge, 1899, Biol. Centrali-Americana Arachnida 2:81.

MALE

Measurements. Based on one male holotype: carapace length 2.05 mm; carapace width 1.30 mm; carapace index 63; sternum length 0.95 mm; sternum width 0.75 mm; sternum index 77.

Femur IV length 1.40 mm; femur IV



width 0.35 mm; leg thickness index 25; leg length index 69.

Abdomen length 2.60 mm; abdomen width 1.15 mm; abdomen index 45.

Embolus length 0.07 mm; bulb length 0.65 mm; male genital index 10.

Description. Carapace orange-brown and hairless, with anterior part of head region dark brown and dark streaking from thoracic groove outwards. Carapace moderately narrow in head region (cephalic width index 58) and smoothly truncated anteriorly. Eyes equal. Thoracic groove moderate.

Abdomen oval, with a full, dark red-brown dorsal sclerite, granulose at anterior end and gradually becoming smooth and shiny posteriorly. Rectangular red-brown sclerite on ventral abdomen. Both pairs of abdominal setae hairlike.

Sternum dark yellow with light, thin setae.

Chelicerae dark brown (like anterior part of carapace). Cheliceral teeth unexamined but probably similar to *C. nanella*.

Coxae all dark yellow. Trochanter IV notch moderate.

Femur I dark brown; rest of leg I and all of leg II light yellow; leg III yellow; leg IV dark yellow, with femur and tibia yellow-brown.

Pedipalp with a distinct tibial apophysis. Tarsus with a globose genital bulb drawn out into a long neck ending with an unpigmented embolus at a right angle near the tip (Fig. 127, 128).

Diagnosis. Castianeira dugesii differs from other *dugesii* group species in the right angle bend at the tip of its embolus.

Remarks. Only a single male is known of this species.

Natural history. Nothing is known of the habits of this species.

Distribution. Only known from the type locality in Guanajuato, Mexico (Map 8).

Records. MEXICO. *Guanajuato.*

Castianeira nanella Gertsch

Figures 129–132, 149, 150. Map 8.

Castianeira nanella Gertsch, 1933, Amer. Mus. Novit. No. 637:6, fig. 3, ♂, from Salt Lake City, Utah; in the American Museum of Natural History, examined.

MALE

Measurements. Based on holotype and 9 males, holotype listed first, range of all follows: carapace length 1.85 mm, 1.75–2.30 mm; carapace width 1.20 mm, 1.15–1.40 mm; carapace index 64, 60–66; sternum length 0.95 mm, 0.90–1.05 mm; sternum width 0.75 mm, 0.70–0.80 mm; sternum index 77, 72–78.

Femur IV length 1.40 mm, 1.40–2.35 mm; femur IV width 0.30 mm, 0.30–0.35 mm; leg thickness index 22, 16–22; leg length index 74, 74–101.

Abdomen length 2.50 mm, 2.30–3.10 mm; abdomen width 1.20 mm, 1.10–1.25 mm; abdomen index 48, 40–51.

Embolus length 0.10 mm, 0.08–0.15 mm; bulb length 0.70 mm, 0.65–0.77 mm; male genital index 14, 12–19.

Description. Carapace dark yellowish brown and hairless. Eyes fairly large, equal, and bordered in black. Carapace narrow in head region (cephalic width index 53–57) and smoothly truncated anteriorly. Thoracic groove moderate.

Abdomen an elongated oval, with a full, shiny, dorsal sclerite—red-brown with a yellow pattern—an anterior horizontal band, a second band connected medially to a short third band, followed by a main horizontal band, followed, finally, by a short, abbreviated stripe. The posterior portion solid red-brown (Fig. 149). Epigastric sclerite orange. Yellow ventral sclerite from epigastric furrow about two thirds of the way to a small inframammilliary sclerite. Anterior pair of abdominal setae very thin and long, posterior pair short and very stout, spinelike.

Sternum dark yellow and hairless. Pedicel very small.

Chelicerae dark yellow-brown, with two moderately small retromargin teeth (the distal one slightly longer) and two promargin teeth, the distal one larger and the proximal one slightly smaller than the retromargin teeth; a small denticle just distal and median to the distal promargin tooth.

Coxa I yellow-brown, coxae II, III, and IV light yellow-brown. Trochanter IV notch not clear.

Legs not attached to type—but apparently femora striped (brown lateral sides and the rest yellow); rest of legs I and II yellow-white, rest of III yellow, with tibia striped. Legs lightly hirsute. Tibia I ventral spination: 3–2, moderate and thin.

Pedipalp with a short, sharp tibial apophysis. Tarsus with a globose genital bulb drawn out into a long neck having a thin embolus and a slight terminal twist (Figs. 131, 132).

FEMALE

Measurements. Based on 11 females: carapace length 1.90–2.60 mm; carapace width 1.20–1.60 mm; carapace index 61–64; sternum length 0.95–1.20 mm; sternum width 0.75–0.95 mm; sternum index 72–81.

Femur IV length 1.65–2.40 mm; femur IV width 0.30–0.45 mm; leg thickness index 18–20; leg length index 86–96.

Abdomen length 2.60–3.75 mm; abdomen width 1.40–2.25 mm; abdomen index 50–63; dorsal sclerite length 0.95–1.55 mm; dorsal sclerite width 0.65–1.15 mm; dorsal sclerite index 64–84.

Description. Carapace light yellow-brown and hairless. Eyes fairly large, bordered in black, and equal. Carapace narrow in head region (cephalic width index 53–59) and smoothly truncated anteriorly. Thoracic groove fairly weak.

Abdomen oval, with moderate, dark yellow-brown dorsal sclerite (about two-

fifths the length of the abdomen) and a light yellow and brown-black pattern—an anterior horizontal band of yellow, a second band connected medially to a short thin band that is connected medially to a major horizontal band, followed finally by a thin horizontal stripe. The posterior two fifths solid brown-black (Fig. 150). Epigastric sclerite yellow-brown. Ventrum light yellow. A small, red-brown inframammilliary sclerite. First pair of abdominal setae long and very thin, second pair moderately heavy and short.

Sternum yellow-orange with sparse, thin setae. Pedicel very small.

Chelicerae yellow-brown, with two moderately large retromargin teeth and two promargin teeth, the distal one slightly larger and the proximal one smaller than the retromargin teeth; a small denticle just distal and medial to the larger promargin tooth.

Coxae all light yellow-brown. Trochanter IV notch moderately weak.

Femur I dark red-brown, femora II–IV striped, with red-brown lateral sides and yellow ventral and dorsal sides. Rest of legs I and II yellow, of leg III dark yellow; leg IV with dark yellow patella, tibia and metatarsus striped like femur, and tarsus yellow-brown. Tibia I ventral spination: 3–3, long and strong.

External female genitalia with a pair of wide, flared openings (Fig. 130). Internal structure with somewhat globose spermathecae drawn out into posterior necks having a distinct crook in them (Fig. 129).

Diagnosis. Castianeira nanella differs from other *dugesii* group species in its genitalia, leg thickness index (18–20), and abdominal pigmentation patterns.

Remarks. Two specimens having fewer dark markings on the abdomen and longer emboli (male genital index 17–19) occur in Mexico.

Natural history. This species has been collected in the dry grass and mesquite regions of Arizona. One egg case collected contained seven eggs.

Distribution. Southwest U.S. and northwest Mexico (Map 8).

Records. Arizona. Cochise Co., Maricopa Co., Pima Co., Santa Cruz Co. *Utah.* Salt Lake Co.

MEXICO. *Sinaloa. Sonora.*

Castianeira alfa new species

Figures 123–126, 151. Map 8.

Holotype. Male from Brawley, Imperial Co., California, 13-VIII-1959 (E. Schlinger); in the American Museum of Natural History. The specific name is an arbitrary combination of letters.

MALE

Measurements. Based on holotype and 9 males, holotype listed first, range of all follows: carapace length 1.85 mm, 1.60–2.15 mm; carapace width 1.20 mm, 1.05–1.40 mm; carapace index 67, 62–67; sternum length 0.85 mm, 0.80–1.00 mm; sternum width 0.70 mm, 0.65–0.75 mm; sternum index 81, 78–85.

Femur IV length 1.40 mm, 1.10–1.60 mm; femur IV width 0.30 mm, 0.30–0.40 mm; leg thickness index 23, 23–26; leg length index 75, 68–76.

Abdomen length 2.30 mm, 1.90–2.75 mm; abdomen width 1.20 mm, 1.00–1.40 mm; abdomen index 51, 49–53.

Embolus length 0.08 mm, 0.07–0.09 mm; bulb length 0.63 mm, 0.60–0.70 mm; male genital index 13, 11–13.

Description. Carapace red-brown, with some sparse white hairs. Eyes moderately small, equal, and bordered in black. Carapace narrower in head region (cephalic width index 55–59) and smoothly truncated anteriorly. Thoracic groove moderate.

Abdomen oval (widening towards posterior) and covered by a full dorsal sclerite —bright red-brown, anterior three-quarters highly punctate, posterior quarter darker

and highly shiny. Whole dorsal sclerite covered with thin, light hairs. Epigastric and ventral sclerites full and red-brown. First pair of abdominal setae hairlike, second pair moderately thin.

Sternum light orange, with extremely sparse, thin setae. Pedicel very short.

Chelicerae orange, with two moderate retromargin teeth (the distal one slightly larger) and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth. A small denticle distal and medial to larger promargin tooth.

Coxae all dark yellow. Trochanter IV notch small.

Femur I dark brown, femora II–IV orange-brown (darker on lateral sides); rest of legs I and II light yellow, rest of leg III light orange-brown, rest of leg IV with patella-tibia orange-brown and slightly striped, metatarsus dark red-brown, and tarsus yellow-brown. Legs moderately hirsute. Tibia I ventral spination: 2–1, small (plus a very small proximal retrolateral spine).

Pedipalp with a rounded, short tibial apophysis. Tarsus with globose genital bulb drawn out into a long neck with a thin embolus, curved at the tip (Fig. 125, 126).

FEMALE

Measurements. Based on 7 females: carapace length 2.40–2.85 mm; carapace width 1.55–1.95 mm; carapace index 65–69; sternum length 1.10–1.30 mm; sternum width 0.85–1.05 mm; sternum index 77–83.

Femur IV length 1.70–2.20 mm; femur IV width 0.40–0.50 mm; leg thickness index 23–25; leg length index 72–78.

Abdomen length 2.85–4.30 mm; abdomen width 1.65–2.50 mm; abdomen index 52–62; dorsal sclerite width 1.20–1.65 mm.

Description. Carapace bright orange-brown and hairless. Eyes moderately small, equal, and bordered in black. Carapace narrower in head region (cephalic width index 59–62) and smoothly truncated anteriorly. Thoracic groove moderate.

Abdomen oval with a moderate, punctate, orange-brown dorsal sclerite. Posterior half brown-black and anterior half light yellow, with a narrow brown-black horizontal band just anterior to the midline (Fig. 151). Epigastric sclerite red-brown. Ventrum pale yellow with some longitudinal brown-black markings from sides of epigastric furrow to a dark area around the spinnerets. First pair of abdominal setae hairlike, second pair moderately thin.

Sternum orange with sparse, thin setae. Pedicel very small.

Chelicerae orange, with two moderate retromargin teeth (the distal one slightly larger) and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth. A small denticle distal and medial to larger promargin tooth.

Coxae all light orange. Trochanter IV notch small.

Femur I dark brown; femora II–IV light orange-brown. Rest of legs I and II yellow-white; rest of III deep yellow; rest of IV light orange-brown. Legs lightly hirsute. Tibia I ventral spination: 2–1, small (plus a very small proximal retrolateral spine).

External epigynum with wide, flared openings (Fig. 124). Internal structure with globose spermathecae narrowing to thin, curved posterior necks (Fig. 123).

Diagnosis. Castianeira alfa differs from other *dugesii* group species in its male and female genitalia (a clear bend at the end of the embolus and small, curved spermatheca1 necks), and in the female abdominal pattern.

Natural history. The type locality is an alfalfa field. Nothing is known of the habits of this species.

Distribution. Southern California, Arizona, and probably adjacent areas in Mexico (Map 8).

Records. Arizona. Yuma Co. *California.* Imperial Co., San Diego Co.

The *athena* Group

Characteristics. Small (male carapace length 1.60–2.30 mm; female carapace length 2.15–2.85 mm), with moderately wide carapace (carapace index 63–68) and moderate cephalic region (male cephalic width index 53–54; female cephalic width index 55–64). Eyes moderately small and approximately equal. Thoracic groove moderate to weak. Carapace and abdomen moderately hirsute.

Discussion. Castianeira athena and *C. rothi* are closely related.

Castianeira athena new species
Figures 172–175, 275. Map 8.

Holotype. Male from Andreas Canyon, Palm Springs, Riverside Co., California, 26-III-1960 (W. J. Gertsch, Ivie and Schrammel); in the American Museum of Natural History. The specific name is a noun in apposition after the Greek goddess Athena.

MALE

Measurements. Based on one male holotype: carapace length 2.30 mm; carapace width 1.55 mm; carapace index 67; sternum length 1.10 mm; sternum width 0.85 mm; sternum index 77.

Femur IV length 1.75 mm; femur IV width 0.50 mm; leg thickness index 27; leg length index 76.

Abdomen length 2.65 mm; abdomen width 1.40 mm; abdomen index 53.

Embolus length 0.11 mm; bulb length 0.77 mm; male genital index 14.

Description. Carapace dark red-brown, with some short light hairs, longer hairs on head region. Head region narrows (cephalic width index 54) and is smoothly truncated anteriorly. Eyes moderate and equal. Thoracic groove moderate.

Abdomen long oval widening posteriorly, with a full, red-brown dorsal sclerite partially covered with long plumose white hairs (many rubbed off) in a striped pattern—two anterior white bands, then an abbreviated band (not reaching lateral sides), and finally a narrow, median, horizontal stripe. Some white hairs at posterior edge of sclerite. Epigastric sclerite light red-brown. Rectangular, light red-brown, ventral sclerite from epigastric furrow to inframammilliary sclerite just anterior to posterior spiracular furrow. Anterior abdominal setae very long and fairly thin, posterior pair short and quite stout. Very short abdominal petiole.

Sternum yellow-brown with very few, heavy setae. Pedicel short.

Chelicerae brown, with two moderate retromargin teeth and two promargin teeth, the distal larger and the proximal slightly smaller than the retromargin teeth. No denticle present.

Coxa I light brown-yellow, II light yellow, III and IV yellow. Trochanter IV notch small.

Femur I dark brown lightening to yellow-white at distal end, femur II brown on lateral sides, yellow dorsally and ventrally; rest of legs I and II very light yellow. Femur III yellow with lateral sides light brown, femur IV dark yellow; rest of III yellow, patella-tibia IV yellow, metatarsus IV very light red-brown, and tarsus IV light yellow. Legs moderately hirsute. Tibia I ventral spination: 3–2, moderately small, proximal spines smaller.

Pedipalp with a small tibial apophysis. Tarsus with a globose genital bulb drawn out into a long neck with a straight, thin, and fairly short embolus (Figs. 174, 175).

FEMALE

Measurements. Based on 11 females: carapace length 2.20–2.85 mm; carapace width 1.40–1.85 mm; carapace index 63–67; sternum length 1.05–1.30 mm; sternum width 0.85–1.00 mm; sternum index 77–84.

Femur IV length 1.65–2.10 mm; femur IV width 0.40–0.60 mm; leg thickness index 24–27; leg length index 73–78.

Abdomen length 2.80–3.65 mm; abdomen

width 1.65–2.65 mm; abdomen index 54–76; dorsal sclerite width 0.75–1.20 mm.

Description. Carapace orange, with some short, light hairs, longer on head region. Carapace narrow in head region (cephalic width index 55–61) and smoothly truncated anteriorly. Eyes moderate, equal, and bordered in black. Thoracic groove moderate.

Abdomen oval, with a small, red-brown dorsal sclerite and a black and white hair pattern—two wide horizontal bands of white hair at anterior end (over sclerite), then an abbreviated wide white band, not continuing off lateral sides, followed by a wide, horizontal, median white band, the third and fourth bands joining in median part. Finally, a posterior band of white hairs; rest of the dorsal abdomen covered with black hairs on light grey ground (Fig. 275). Light red-brown epigastric sclerite. Ventral abdomen light grey. A small red-brown inframammilliary sclerite. Anterior abdominal setae very thin and long, posterior pair thicker and stouter.

Sternum yellow-brown, with sparse, very long setae. Pedicel fairly short.

Chelicerae light brown, with two moderate retromargin teeth and two promargin teeth, the distal larger and the proximal slightly smaller than the retromargin teeth. No denticle present.

Coxae I, II, and III yellow-white, IV yellow. Trochanter IV notch small.

Femora I dark brown and II brown except yellow-white distal end; rest of legs I and II very light yellow. Femora III and IV deep yellow with dark hairs on sides; rest of leg III dark yellow; patella-tibia IV dark yellow with dark hairs; metatarsus IV red-brown, and tarsus IV light red-brown. Legs moderately hirsute. Tibia I ventral spination: 3–2, moderately small.

External epigynum with very small circular openings near anterior end of spermathecae (Fig. 173). Internal structure with heavily rounded spermathecae with thick posterior necks (Fig. 172).

Diagnosis. The females of *Castianeira athena* have very small epigynal openings (Fig. 173) and a distinctive abdominal hair pattern. The males differ from other *Castianeira* in their small size, embolus, and carapace of a single color.

Remarks. Castianeira athena is closely related to *C. rothi* but is somewhat larger and differs in genitalic characters.

Natural history. Nothing is known of the habits of this species. An egg case collected with a female consisted of two disc-like white cases affixed to one another, one case with 27 eggs and the other with 19.

Distribution. Southern California and northwest Mexico (Map 8).

Records. California. Inyo Co., Los Angeles Co., Riverside Co., San Bernadino Co., San Diego Co.

MEXICO. *Baja California.*

Castianeira rothi new species

Figures 208–211, 274. Map 8.

Holotype. Male from South Fork of the Cave Creek, Chiricahua Mountains, Cochise Co., Arizona, 18-V-1966 (J. Reiskind); in the Museum of Comparative Zoology. The species is named after Vincent D. Roth.

MALE

Measurements. Based on holotype and 3 males, holotype listed first, range of all follows: carapace length 1.75 mm, 1.60–1.75 mm; carapace width 1.15 mm, 1.10–1.15 mm; carapace index 67, 63–68; sternum length 0.85 mm, 0.75–0.85 mm; sternum width 0.70 mm, 0.65–0.70 mm; sternum index 81, 81–85.

Femur IV length 1.35 mm, 1.25–1.40 mm; femur IV width 0.30 mm, 0.30 mm; leg thickness index 24, 23–26; leg length index 78, 76–81.

Abdomen length 2.10 mm, 2.05–2.15 mm; abdomen width 1.20 mm, 1.05–1.20 mm; abdomen index 57, 52–57.

Embolus length 0.10 mm, 0.08–0.10 mm; bulb length 0.57 mm, 0.54–0.59 mm; male genital index 17, 15–18.

Description. Carapace with orange-brown thoracic region with short, light hairs and a dark brown cephalic region with moderately long, light hair. Head narrows (cephalic width index 53–54) and is smoothly truncated anteriorly. Eyes moderate and equal. Thoracic groove moderately weak.

Abdomen oval, widening posteriorly with a full, punctate, maroon-brown dorsal sclerite with short, plumose hairs—three faint, yellowish, horizontal hair bands, two at anterior end and one at median (Fig. 274). Epigastric sclerite red-brown. A full, rectangular, red-brown ventral sclerite and a small red-brown inframammilliary sclerite. First pair of abdominal setae very thin, second pair moderately thin.

Sternum shield-shaped and dark yellow-brown, with sparse, thin setae. Pedicel very short. Abdominal petiole very short but present.

Chelicerae light brown-black, with two moderate retromargin teeth and two promargin teeth, the distal larger and the proximal smaller than the retromargin teeth; with a very small denticle just medial and distal to the larger promargin tooth.

Coxa I light yellow-brown, II and III light yellow, IV yellow. Trochanter IV notch small.

Femur I dark brown, lightening at distal end, femora II–IV yellow with brown lateral sides. Rest of legs I and II light yellow, rest of III dark yellow, patella-tibia IV orange, metatarsus IV dark red-brown, tarsus IV light yellow-brown. Tibia I ventral spination: 2–1, small. Legs lightly hirsute.

Pedipalp with a blunt, short tibial apophysis. Tarsus with globose genital bulb drawn out into a long neck with straight, moderately sclerotized embolus with a distinct twist at the tip (Fig. 210, 211).

FEMALE

Measurements. Based on 10 females: carapace length 2.15–2.50 mm; carapace width 1.40–1.60 mm; carapace index 65–68; sternum length 1.00–1.10 mm; sternum width 0.85–0.95 mm; sternum index 80–85.

Femur IV length 1.60–1.85 mm; femur IV width 0.40–0.50 mm; leg thickness index 24–27; leg length index 74–79.

Abdomen length 2.60–3.50 mm; abdomen width 1.60–2.75 mm; abdomen index 60–78; dorsal sclerite length 1.00–1.10 mm; dorsal sclerite width 0.95–1.20 mm; dorsal sclerite index 83–109.

Description. Carapace with red-brown thoracic region with short, light hairs and a dark red-brown cephalic region with moderately long, light hairs. Head narrow (cephalic width index 55–64) and smoothly truncated anteriorly. Eyes moderate and equal. Thoracic groove moderately weak.

Abdomen a wide oval and brown, with a moderately small maroon sclerite. A faint, light, horizontal band just anterior to median of abdomen. Epigastric sclerite red-brown. Ventrum with two faint beaded stripes from sides of epigastric furrow to spinnerets. First pair of abdominal setae very thin, second pair moderately thin.

Sternum shield-shaped, orange, with sparse, thin setae. Pedicel very short.

Chelicerae red-brown, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth; with a very small denticle just medial and distal to the larger promargin tooth.

Coxa I yellow-brown, II, III, and IV deep yellow. Trochanter IV notch small.

Femur I dark brown, lighter at distal end, femora II–IV yellow with brown lateral sides. Rest of legs I and II light yellow, of leg III yellow, patella-tibia IV yellow-brown, metatarsus IV red-brown, tarsus IV yellow. Tibia I ventral spination: 3–2, moderate. Legs lightly hirsute.

External epigynum with widely separated circular openings (Fig. 209). Internal structure with rounded saclike spermathecae having thick posterior necks (Fig. 208).

Diagnosis. Castianeira rothi differs from

other members of the *athena* group in its genitalic characters and in having its cephalic region darker than the thoracic region.

Remarks. This species is closely related to *C. athena* but is smaller and has distinctive genitalia (females) and color and hair patterns.

Natural history. C. rothi is found in the mountainous oak forests of southern Arizona.

Distribution. Southern Arizona (Map 8).

Records. Arizona. Cochise Co., Santa Cruz Co.

The *dorsata* Group

Characteristics. Large (male carapace length 2.85–4.60 mm; female carapace length 2.85–5.40 mm), with a carapace index 65–69. Abdomen covered with black and white, and yellow or orange plumose hairs. Epigynum with a pair of fairly high openings, with the bursae copulatrices more or less passing over the globose anterior of the spermathecae. Male genital index 22–38. Eyes moderately small and approximately equal (anterior median eyes sometimes slightly larger than laterals).

Discussion. This Mexican and Central American group is easily distinguished by the genitalia—very long emboli and distinctive bursae copulatrices.

Castianeira dorsata (Banks)

Figures 133–136, 148. Map 9.

Thargalia dorsata Banks, 1898, Proc. California Acad. Sci. (3)1(7):228, pl. 13, fig. 30, ♀, ♂. Male and female cotypes from San José del Cabo, Sierra San Nicolas, and Sierra San Lazaro in Baja California, Mexico; in the California Academy of Sciences; destroyed, and the Museum of Comparative Zoology; examined. Male lectotype from Sierra San Lazaro chosen.

MALE

Measurements. Based on lectotype and 6 males, lectotype listed first, range of all follows: carapace length 3.95 mm, 3.10–

4.60 mm; carapace width 2.60 mm, 2.00–2.95 mm; carapace index 66, 65–69; sternum length 1.75 mm, 1.40–2.05 mm; sternum width 1.40 mm, 1.10–1.55 mm; sternum index 80, 78–83.

Femur IV length 2.85 mm, 2.55–3.70 mm; femur IV width 0.85 mm, 0.65–0.95 mm; leg thickness index 30, 25–30; leg length index 72, 72–83.

Abdomen length 4.10 mm, 3.35–5.10 mm; abdomen width 2.15 mm, 1.55–2.40 mm; abdomen index 53, 46–53.

Embolus length 0.26 mm, 0.26–0.29 mm; bulb length 1.20 mm, 1.10–1.28 mm; male genital index 22, 22–25.

Description. Carapace red-brown with a wide longitudinal median stripe of white hairs and a lighter pigmented spot just anterior to the thoracic groove. Head narrow (cephalic width index 53–60) and smoothly truncated anteriorly. Eyes moderate and equal. Thoracic groove moderate.

Abdomen a long oval with a full dorsal sclerite, orange medially, orange-brown on sides, and covered with fairly long white hairs. Epigastric sclerite maroon over book-lungs but orange at center. An almost full, rectangular, orange ventral sclerite and a small orange-brown inframammilliary sclerite. First pair of abdominal setae hair-like, second pair very thin.

Sternum shield-shaped and orange, with sparse, thin setae. Pedicel very short.

Chelicerae red-brown with two moderate retromargin teeth and two promargin teeth, the distal one much larger and the proximal one smaller than the retromargin teeth. No denticle present.

Coxae all orange-brown. Trochanter IV notch moderately small.

Femora all red-brown. Rest of legs I and II yellow-orange; rest of legs III and IV orange except tarsi yellow. Tibia I ventral spination: 3–2, moderate. Legs heavily hirsute.

Pedipalp with a short, sharp tibial apophysis. Tarsus with globose genital bulb drawn out into a long neck with a long, straight, thin, sclerotized embolus with a distinct twist at the tip (Figs. 134, 135).

FEMALE

Measurements. Based on 5 females: carapace length 3.95–4.55 mm; carapace width 2.60–2.95 mm; carapace index 65–68; sternum length 1.65–1.95 mm; sternum width 1.40–1.55 mm; sternum index 79–83.

Femur IV length 2.95–3.30 mm; femur IV width 0.85–0.95 mm; leg thickness index 28–29; leg length index 72–80.

Abdomen length 4.20–5.60 mm; abdomen width 2.40–4.15 mm; abdomen index 58–77; dorsal sclerite length 0.55–0.95 mm; dorsal sclerite width 1.10–1.50 mm; dorsal sclerite index 153–206.

Description. Carapace deep red-brown with a wide longitudinal median stripe of white hair. Head narrow (cephalic width index 60–63) and smoothly truncated anteriorly. Eyes moderate and equal. Thoracic groove moderately strong.

Abdomen oval, with a small red-brown dorsal sclerite (white hairs on the sclerite) and a wide longitudinal band of orange hair with brownish hairs on the sides (Fig. 148). Epigastric and small inframammilliary sclerites red-brown. Ventrum with two beaded stripes from sides of epigastric furrow to the posterior sclerite. First pair of abdominal setae very thin, second pair thin.

Sternum shield-shaped and red-brown, with sparse, thin setae. Pedicel very short.

Chelicerae deep red-brown, with two moderate retromargin teeth and two promargin teeth, the distal one much larger and the proximal one smaller than the retromargin teeth. No denticle present.

Coxae all red-brown. Trochanter IV notch moderately small.

Legs all red-brown, with legs I and II distal to the femora and all tarsi slightly lighter. Tibia I ventral spination: 3–2, moderately strong. Legs heavily hirsute.

External epigynum with two small, widely separated, round openings (Fig.

136), internal structure with rounded spermathecae and short posterior necks, the bursae copulatrices close to the spermathecae (Fig. 133).

Diagnosis. Castianeira dorsata differs from other *dorsata* group species in having small, medially directed epigynal openings (in the female) and an abdomen without any yellow or white spots (in the male).

Remarks. The red-orange hair band on the abdomen is often broken horizontally in several places, especially near the posterior end, and also often extends down the sides. The distinctive female genitalia distinguishes this species from others that look superficially like it—*Castianeira ornata* (in the *longipalpus* group) and *C. occidens* (in the *descripta* group). The convergent pattern of a red-orange abdomen and often a longitudinal band of white hairs on the carapace may be the result of selection for mutillid wasp mimicry, but there are no field observations either to support or to refute this, except those of Scheffer (1906) (see *Natural history,* under *Castianeira descripta*).

Natural history. Nothing is known of the habits of this species.

Distribution. Southwestern U.S. and northwestern Mexico (Map 9).

Records. Arizona. Cochise Co., Yuma Co.

MEXICO. *Baja California., Jalisco., Michoacan., Morelos., Nayarit., Nuevo Leon., Sinaloa., Sonora.*

Castianeira stylifera Kraus

Figures 145–147, 159. Map 9.

Castianeira stylifera Kraus, 1955, Abhandl. Senckenb. Naturf. Ges. 493:49–50, figs. 128–130, ♂, ♀. Male holotype from Finca La Yoya, Sonsonate, El Salvador; in the Senckenberg Museum, examined.

MALE

Measurements. Based on one male holotype: carapace length 4.55 mm; carapace width 2.95 mm; carapace index 65; sternum length 2.05 mm; sternum width 1.55 mm; sternum index 75.

Femur IV length 3.55 mm; femur IV width 0.95 mm; leg thickness index 27; leg length index 78.

Abdomen length 5.10 mm; abdomen width 2.20 mm; abdomen index 43.

Embolus length 0.39 mm; bulb length 1.61 mm;; male genital index 24.

Description. Carapace dark red-brown, with short, sparse white hairs except "head" lighter red-brown and covered with longer white hair. Lateral edges of carapace bordered in heavy white hair except in head region. Eyes equal and bordered in black. Head narrow (cephalic width index 59) and smoothly truncated anteriorly.

Abdomen very long and oval, with a full dorsal sclerite, red-brown except for a large central spot and a posterior spot of dark yellow, and covered with plumose white hairs. Epigastric sclerite light red-brown. A rectangular red-brown ventral sclerite from epigastric furrow to an inframammilliary sclerite. Abdominal setae very thin. Pedicel very short.

Sternum light red-brown, with very long, thin setae.

Chelicerae light red-brown, with two moderate retromargin teeth and two promargin—the distal one larger and the proximal one smaller than the retromargins. A denticle possibly present.

Coxae all yellow-brown. Trochanter IV notch moderate.

Femora I and II brown, patellae I and II yellow-brown, rest of I and II light yellow. Leg III dark yellow-brown, with a darker brown ring in center of tibia and lighter tarsus. Femur IV brown, rest of IV dark yellowish brown, with a dark brown, wide ring in the center of tibia and lighter tarsus. Legs heavily hirsute, with patches of white hairs on femora, and moderately heavily spiney. Tibia I ventral spination: 3–2.

Pedipalp with a moderate tibial apophysis. Tarsus with a globose genital bulb drawn out into a long neck with a long, heavily sclerotized embolus tip (Fig. 147).

FEMALE

Measurements. Based on 2 females: carapace length 4.55–5.40 mm; carapace width 2.95–3.65 mm; carapace index 65–67; sternum length 2.00–2.30 mm; sternum width 1.60–1.75 mm; sternum index 77–79.

Femur IV index 3.30–3.85 mm; femur IV width 1.00–1.20 mm; leg thickness index 30–31; leg length index 72–73.

Based on one female only: abdomen length 6.90 mm; abdomen width 4.40 mm; abdomen index 64.

Description. Carapace dark purplish red-brown covered with light hairs, especially long and dense on cephalic region, and lateral edges of thoracic region bordered with heavy white hair. Head narrow (cephalic width index 62) and smoothly truncated anteriorly. Eyes almost equal, with darker borders.

Abdomen oval, with small, red-brown, anterior dorsal sclerite, and covered with light yellow and black plumose hairs; anterior end black with some white hairs, then a wide horizontal light band continuing posteriorly along median to another wide band, thereby providing two large dark lateral spots, and a wide black posterior end (Fig. 159). Epigastric sclerite red-brown. Ventral abdomen with two faint, longitudinal, beaded stripes from sides of epigastric furrow posteriorly. Anterior abdominal setae hairlike, posterior pair very thin. Pedicel short.

Sternum dark red-brown, with long, fairly thin setae.

Chelicerae dark red-brown, with two medium retromargin teeth and two promargin teeth, the distal one larger and the proximal smaller than the retromargins. A denticle possibly present.

Coxae all red-brown. Trochanter IV notch moderate.

All femora dark red-brown; patellae I and II light red-brown, rest of legs I and II yellow. Rest of legs III and IV dark red-brown with lighter tarsi. Legs moderately hirsute, with white hair patches on femora and legs III and IV, and moderately heavy spination. Tibia I ventral spination: 3–2.

External epigynum with small semicircular openings (Fig. 146). Internal structure highly sclerotized, with saclike spermathecae and with bursae copulatrices passing over anterior end of spermathecae (Fig. 145).

Diagnosis. The males of *Castianeira stylifera* differ from those of other *dorsata* group species in their genitalia (male genital index 24) and light abdominal spots. The females differ from the others in their epigynal openings (smaller than those of *C. azteca*) and abdominal pattern (which is similar to *C. azteca*).

Remarks. This species is closely related to *Castianeira azteca* but is much larger and has distinct genitalia. The yellow (much redder in the living spider) abdominal spots may be of mimetic (to mutillid wasps) value.

Natural history. Nothing is known of the habits of this species.

Distribution. El Salvador (Map 9).

Castianeira azteca new species
Figures 137–141, 156. Map 9.

Holotype. Male from La Planta de Moctezuma, near Fortin, Veracruz, Mexico, 7-VII-1947 (C. and M. Goodnight); in the American Museum of Natural History. The specific name is an adjective from the name given to Indians of the Nahuatlan tribe which founded the pre-Columbian Mexican Empire.

MALE

Measurements. Based on holotype and 5 males, holotype listed first, range of all follows: carapace length 3.90 mm, 2.85–4.25 mm; carapace width 2.60 mm, 1.90–2.80 mm; carapace index 67, 65–69; sternum length 1.75 mm, 1.30–1.90 mm; sternum width 1.35 mm, 1.05–1.40 mm; sternum index 76, 74–80.

Femur IV length 2.95 mm, 2.40–3.20

mm; femur IV width 0.90 mm, 0.60–0.95 mm; leg thickness index 30, 25–30; leg length index 76, 75–83.

Abdomen length 4.55 mm, 3.40–4.75 mm; abdomen width 1.95 mm, 1.50–2.40 mm; abdomen index 43, 43–53.

Embolus length 0.47 mm, 0.42–0.52 mm; bulb length 1.44 mm, 1.16–1.56 mm; male genital index 33, 32–38.

Description. Carapace maroon, granulose, and covered with white plumose hairs in a wide longitudinal band over the thoracic region and widening to cover the cephalic region with longer hairs. Head narrows (cephalic width index 53–55) and is smoothly truncated anteriorly. Eyes moderately small and equal. (Anterior medians slightly larger than laterals.) Thoracic groove strong.

Abdomen a long oval, with a full, dark red-brown dorsal sclerite (with two lighter spots, one in middle and one at posterior) covered with a very wide longitudinal band of heavy white hairs. Epigastric sclerite and small inframammilliary sclerite dark red-brown, three-quarters rectangular ventral sclerite red-brown with some white hairs. Both pairs of abdominal setae thin.

Sternum shield-shaped and red-brown, with sparse, long, thin setae. Pedicel very short.

Chelicerae dark red-brown, with two moderately large retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth; a very minute denticle just median and distal to the larger promargin tooth.

Coxae all dark orange-brown. Trochanter IV notch moderately strong.

Femora all dark red-brown, with abundant white hair. Rest of legs I and II yellow-orange; rest of legs III and IV dark red-brown (III slightly lighter), with yellow-orange tarsi. Legs heavily hirsute. Tibia I ventral spination: 3–2, moderately long and strong.

Pedipalp with a short, fairly blunt, tibial apophysis. Tarsus with a globose genital bulb drawn out into a long neck with a very long and slightly curved sclerotized embolus (Fig. 139–141).

FEMALE

Measurements. Based on 2 females: carapace length 3.50–4.60 mm; carapace width 2.35–2.95 mm; carapace index 65–68; sternum length 1.55–1.95 mm; sternum width 1.25–1.55 mm; sternum index 79–81.

Femur IV length 2.70–3.15 mm; femur IV width 0.75–1.05 mm; leg thickness index 29–33; leg length index 69–78.

Abdomen length 3.85–4.45 mm; abdomen width 2.30–2.65 mm; abdomen index 59–60; dorsal sclerite length 0.40–0.85 mm; dorsal sclerite width 1.05–1.65 mm; dorsal sclerite index 190–250.

Description. Carapace orange, granulose, and covered with black and white plumose hairs in a wide longitudinal band over the thoracic region, widening to cover the cephalic region with longer hairs. Head narrows (cephalic width index 58–59) and is smoothly truncated anteriorly. Eyes moderately small, equal, and bordered in black. Thoracic groove moderately strong.

Abdomen a large oval with a small, red-brown dorsal sclerite and a black and orange hair pattern with some white hairs on the sclerite—wide longitudinal orange hair band from sclerite to area just anterior to spinnerets and extending somewhat laterally at middle and at posterior end (Fig. 156), abundant white hair spots on sides of abdomen. Epigastric sclerite light orange. Ventrum with a pair of light lines from sides of epigastric furrow to a small, orange-brown, inframammilliary sclerite. First pair of abdominal setae very thin, second pair thin.

Sternum shield-shaped, orange, with long, thin setae.

Chelicerae orange-brown, with two moderately large retromargin teeth and two

promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth; a very small denticle just median and distal to the larger promargin tooth.

Coxae all light yellow-orange. Trochanter IV notch moderate.

All femora light orange; rest of legs I and II light yellow; rest of legs III and IV light orange, but with center half of tibia IV and all of metatarsus IV light orange-brown. Legs moderately heavily hirsute. Tibia I ventral spination: 2–2, moderate length and heavy.

External epigynum with two semicircular, slitlike openings directed posteriorly and slightly medially (Fig. 138). Internal structure with rounded spermathecae having thick posterior necks and bursae copulatrices looping over anterior ends of spermathecae (Fig. 137).

Diagnosis. Castianeira azteca closely resembles *C. stylifera* but differs from it in male genitalia (male genital index 32–38), in female genitalia (epigynal openings larger than in *C. stylifera*), and in size (*C. azteca* smaller than *C. stylifera*).

Remarks. There is considerable variation in this species. Males from Veracruz and Oaxaca have shorter emboli (male genital index 32–33) than do those from Guerrero (male genital index 35–38), and the abdominal spots vary in length and width in the two females. These spiders may be mutillid wasp mimics.

Natural history. Nothing is known of the habits of this species.

Distribution. Mexico (Map 9).

Records. MEXICO. *Nayarit., Oaxaca., Veracruz.*

Castianeira luctuosa O. P.-Cambridge

Figures 142, 152. Map 9.

Castianeira luctuosa O. P.-Cambridge, 1898, Biol. Centrali-Americana Arachnida 1:287, pl. 32, fig. 9, ♀, from Amula, Guerrero, Mexico; in the British Museum (Natural History), examined.

FEMALE

Measurements. Based on one female holotype: carapace length 2.85 mm; carapace width 1.85 mm; carapace index 66; sternum length 1.30 mm; sternum width 1.05 mm; sternum index 81.

Femur IV length 2.35 mm; femur IV width 0.60 mm; leg thickness index 25; leg length index 83.

Abdomen length 3.10 mm; abdomen width 2.00 mm; abdomen index 64; dorsal sclerite length 1.40 mm; dorsal sclerite width 1.20 mm; dorsal sclerite index 86.

Description. Carapace dark red-brown, slightly lighter red-brown in head region, uniformly covered with moderately dense white hair. Carapace moderately narrow in head region (cephalic width index 65) and smoothly truncated anteriorly. Eyes bordered in black, and posterior eyes equal, whereas anterior median eyes moderately larger than anterior lateral eyes. Thoracic groove relatively weak.

Abdomen oval, with a large, orange-brown dorsal sclerite (about two-fifths of the way from anterior end) and a light brown and white dorsal hair pattern—two horizontal anterior white bands, a short median sinuous horizontal white bar, a median white band, two pairs of small horizontal white spots, and a posterior white hair band (Fig. 152). Ventral abdomen yellow with two faint longitudinal lines. On each side of abdomen two large white hair spots—one below mid-band and one below anterior sclerite. Anterior abdominal setae thin, posterior pair moderately thin (fairly thick at base).

Sternum light brown, with thin setae. Pedicel negligible.

Chelicerae light brown, with two moderate retromargin teeth and two promargin teeth, the distal one slightly longer and the proximal one slightly smaller than the retromargin teeth.

Coxae all yellow-brown. Trochanter IV notch moderate.

Femora light brown; rest of legs I and II light yellow; rest of leg III yellow, with metatarsus darker; rest of leg IV light brown, with ends of tibia much lighter and tarsus yellow. Legs moderately hirsute.

External epigynum with moderately small, anteriorly and laterally oriented, slitlike openings (Fig. 142). Internal structure with typical inverted pear-shaped spermathecae.

Diagnosis. The epigynal openings (moderately small and directed anteriorly and laterally) and abdominal white hair pattern distinguish this species from all other *Castianeira.*

Natural history. Nothing is known of the habits of this species.

Distribution. Only known from the type locality in Guerrero, Mexico (Map 9).

Records. MEXICO. *Guerrero.*

THE *TRUNCATA* GROUP

Castianeira truncata Kraus

Figures 205, 206. Map 10.

Castianeira truncata Kraus, 1955, Abhandl. Senckenb. Naturf. Ges. 493:48–49, figs. 126–127, ♂, from Finca El Carmen, San Vincente, El Salvador; in the Senckenberg Museum, examined.

MALE

Measurements. Based on one male holotype: carapace length 2.05 mm; carapace width 1.35 mm; carapace index 67; sternum length 0.95 mm; sternum width 0.80 mm; sternum index 85.

Femur IV length 1.60 mm; femur IV width 0.45 mm; leg thickness index 29; leg length index 78.

Abdomen length 2.65 mm; abdomen width 1.35 mm; abdomen index 51.

Embolus length 0.09 mm; bulb length 0.63 mm; male genital index 14.

Description. Carapace dark red-brown, with short white hairs over total surface. Head region narrow (cephalic width index 54) and smoothly truncated anteriorly. Posterior eyes equal, anterior median eyes somewhat larger than anterior lateral eyes, and all eyes bordered in black. Thoracic groove fairly weak.

Abdomen long, oval, widening posteriorly, with a full, maroon dorsal sclerite covered with white hairs (many rubbed off). Epigastric sclerite dark red-brown. Wide, rectangular, dark red-brown ventral sclerite from epigastric furrow to a small inframammilliary red-brown sclerite. Anterior abdominal setae very thin and long, posterior pair much shorter, stouter, and close to abdomen. Abdominal petiole short but distinct.

Sternum red-brown, with sparse, light, hairlike setae. Pedicel short.

Chelicerae red-brown, with two fairly small retromargin teeth and two promargin teeth, the distal one larger and the proximal one a bit smaller than the retromargin teeth. A denticle probably present.

Coxa I very light brown, coxae II and III yellow, and coxa IV yellow-brown. Trochanter IV notch small.

Femora I and II brown at base, grading to light yellow at distal end and on dorsal side; rest of legs I and II light yellow. Femur, patella-tibia, and metatarsus III dark brown on lateral sides and yellow-brown on dorsum and ventrum, tarsus III light yellow. Femur IV dark brown with light distal end, patella-tibia dark brown with a very light distal end, metatarsus IV dark brown, tarsus IV yellow-brown. Legs moderately hirsute. Tibia I ventral spination: 2–1.

Pedipalp with a small tibial apophysis. Tarsus with a globose genital bulb drawn out into a long neck and ending with a lightly sclerotized, blunt-ended embolus (Figs. 205, 206).

Diagnosis. The short, clublike embolus (Fig. 206) and the small size of *C. truncata* distinguish it from all other *Castianeira.*

Natural history. Nothing is known of the habits of this species.

Distribution. El Salvador (Map 10).

The *dubia* Group

Characteristics. Moderately large (male carapace length 2.15–2.95 mm; female carapace length 2.95–3.90 mm), with a carapace index 54–60 (fairly narrow). Abdomen elongate, especially in the male (male abdomen index 30–38). Spermathecae with globose anterior ends and moderately thin posterior necks. Eyes moderately large, with the anterior median eyes much larger than the rest.

Discussion. This group and the three single species groups following it are large *Castianeira*, with anterior median eyes much larger than the laterals. This eye character is common in larger neotropical *Castianeira* and is one of the major characters used in the original description of the genus (Keyserling, 1879).

Castianeira dubia (O. P.-Cambridge), new combination. Figures 168–171, 182, 183. Map 10.

Corinnomma dubium O. P.-Cambridge, 1898, Biol. Centrali-Americana Arachnida 1:277, pl. 34, fig. 1, ♀, from Teapa, Tabasco, Mexico; in the British Museum (Natural History), examined.

Myrmecotypus dubius: F. P.-Cambridge, 1899, Biol. Centrali-Americana Arachnida 2:84.

Castianeira nitida Chickering, 1937, Trans. Amer. Microscop. Soc. 56(1):6–7, figs. 7, 46, 50, ♂, from Barro Colorado Island, Panama Canal Zone; in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

MALE

Measurements. Based on 10 males: carapace length 2.15–2.95 mm; carapace width 1.30–1.70 mm; carapace index 57–60; sternum length 1.10–1.40 mm; sternum width 0.75–0.95 mm; sternum index 63–70.

Femur IV length 1.65–2.30 mm; femur IV width 0.40–0.50 mm; leg thickness index 23–25; leg length index 65–80.

Abdomen length 3.20–2.90 mm; abdomen width 1.10–1.35 mm; abdomen index 34–38.

Embolus length 0.03 mm; bulb length 0.78–0.98 mm; male genital index 3–4.

Description. Carapace long, red-brown, with fine light hairs and slightly darker on sides. Head narrow (cephalic width index 50–59) and smoothly truncated anteriorly. Eyes somewhat raised, posterior eyes moderate and equal, anterior median eyes larger, and anterior lateral eyes much smaller. Eyes bordered in black. Carapace quite narrow posteriorly. Thoracic groove moderate.

Abdomen elongated, with an almost full, dark red-brown dorsal sclerite and a pattern of white hairs surrounded by golden-brown hairs—a wide anterior horizontal band followed by a pair of spots, then a thin median band and a wide posterior band (Fig. 183). Epigastric and a large ventral sclerite dark red-brown. A small red-brown inframammilliary sclerite. First pair of abdominal setae hairlike, second pair moderate.

Sternum shield-shaped, long, and orange-brown, with some fine light hairs. Short pedicel.

Chelicerae orange-brown, with two moderate retromargin teeth and two promargin teeth, the distal larger and the proximal smaller than the promargin teeth; a very small denticle just distal and medial to the larger promargin tooth.

Coxae all light yellow-white. Trochanter IV notch moderately small.

Femora I and II striped—yellow with brown lateral sides; femur III also striped—yellow with light brown sides; femur IV light red-brown. Rest of legs I and II light yellow-white (slightly brown sides); rest of leg III light yellow; rest of leg IV—patella yellow, tibia striped yellow with red-brown sides and yellow distal end. Metatarsus red-brown, tarsus yellow. Legs moderately lightly hirsute. Tibia I ventral spination: 3–2, small.

Pedipalp with a short, blunt tibial apophysis. Tarsus with a globose genital bulb drawn out into a long neck with a very small, conical, sclerotized embolus tip with a distinct twist (Figs. 170, 171).

FEMALE

Measurements. Based on holotype and 10 females, holotype listed first, but not included in range of rest which follows: carapace length 3.20 mm, 3.30–3.90 mm; carapace width 1.75 mm, 1.95–2.30 mm; carapace index 54, 57–59; sternum length 1.45 mm, 1.55–1.80 mm; sternum width 0.95 mm, 1.10–1.20 mm; sternum index 64, 66–72.

Femur IV length 2.20 mm, 2.40–2.95 mm; femur IV width 0.55 mm, 0.60–0.70 mm; leg thickness index 25, 23–26; leg length index 68, 71–77.

Abdomen length 4.65 mm, 3.35–5.55 mm, abdomen width 2.10 mm, 1.75–3.10 mm; abdomen index 45, 52–64; dorsal sclerite length 1.50 mm, 1.30–1.50 mm; dorsal sclerite width 0.85 mm, 0.85–1.05 mm; dorsal sclerite index 59, 62–75.

Description. Carapace long, dark red-brown, with fine light hairs, and cephalic region slightly lighter. Head narrow (cephalic width index 59–65) and smoothly truncated anteriorly. Eyes slightly raised, posterior eyes moderately small and equal, anterior median eyes larger, and anterior lateral eyes much smaller. Eyes bordered in black. Carapace quite narrow posteriorly. Thoracic groove moderately small.

Abdomen elongated oval, with a moderately small, long, red-brown dorsal sclerite and covered with yellow-white and brown hairs. Light hair pattern—cross band over sclerite followed by a short stripe, a thin median stripe, and a wide posterior stripe (Fig. 182). Epigastric sclerite red-brown. A pair of light lines from sides of epigastric furrow to a small, brownish, inframammilliary sclerite. First pair of abdominal setae hairlike and very long, second pair moderate and short.

Sternum shield-shaped, long, and dark red-brown, with fine, long hairs. Short pedicel.

Chelicerae red-brown, with two moderate retromargin teeth and two promargin teeth, the distal larger and the proximal smaller than the promargin teeth; a very small denticle just distal and medial to the larger promargin tooth.

Coxae all light yellow-white (IV slightly darker). Trochanter IV notch moderately small.

Femora I and IV red-brown, lightening at distal end, femora II and III striped—yellow with red-brown sides. Rest of legs I and II—patellae-tibiae yellow-white, metatarsi and tarsi yellow; rest of leg III—patella-tibia striped like femur, metatarsus orange, tarsus yellow; rest of leg IV—patella orange, tibia dark red-brown with distal orange tips, metatarsus dark red-brown, tarsus dark yellow-brown. Legs moderately hirsute. Tibia I ventral spination: 3–2, moderate.

External epigynum with two small openings (Fig. 169). Internal structure with globose spermathecae having fairly narrow posterior necks (Fig. 168).

Diagnosis. Males of *Castianeira dubia* differ from other *Castianeira* in their genitalia (very small conical embolus), abdominal pattern, and abdomen index (34–38). The females have a wide posterior band of yellow-white hairs on the abdomen.

Remarks. The Mexican form (the holotype) has slightly smaller epigynal openings and a narrower posterior stripe. This abdominal pattern may be associated with mutillid wasp mimicry.

Natural history. Nothing is known of the habits of this species.

Distribution. Southern Mexico and Central America (Map 10).

Records. MEXICO. *Tabasco.*

COSTA RICA. Turrialba.

PANAMA. Bocas del Toro, Portobelo.

CANAL ZONE. Barro Colorado Island, Madden Dam Forest.

Castianeira zembla new species

Figures 176, 177, 187. Map 10.

Holotype. Male from Ocosingo, Chiapas, Mexico, 25-VI-1950 (C. and M. Goodnight,

and L. J. Stannard); in the American Museum of Natural History. The specific name is a noun in apposition from the name of a fictitious country in "Pale Fire" by Vladimir Nabokov.

MALE

Measurements. Based on one male holotype: carapace length 2.95 mm; carapace width 1.65 mm; carapace index 56; sternum length 1.55 mm; sternum width 0.95 mm; sternum index 60.

Femur IV length 2.15 mm; femur IV width 0.55 mm; leg thickness index 27; leg length index 71.

Abdomen length 4.10 mm; abdomen width 1.25 mm; abdomen index 30.

Embolus length 0.10 mm; bulb length 0.86 mm; male genital index 11.

Description. Carapace deep, almost black, maroon; slightly lighter in head region, hairless, with a punctate surface. Head narrow (cephalic width index 56) and smoothly truncated anteriorly. Eyes equal and moderate, except anterior median eyes about twice as large as the anterior lateral eyes. Thoracic groove moderately strong.

Abdomen with a full, dark maroon dorsal sclerite, cylindrical, very narrow and long, and pinched very slightly in middle (Fig. 187). Anterior portion with some white hairs, and whole surface punctate. Epigastric sclerite maroon, and elongated rectangular ventral sclerite red-brown (slightly constricted in middle). Small red-brown inframammilliary sclerite. First pair of abdominal setae extremely thin, second pair thin. Short but distinct abdominal petiole.

Sternum shield-shaped, fairly long, red-brown, punctate and almost setae-less. Pedicel short.

Chelicerae brown, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth. A small distinct denticle medial and distal to larger promargin tooth.

Coxae I and II very light yellow-brown, III yellow-brown, IV base brown, lightening at distal end. Trochanter IV with a moderate curved notch.

Femora I, III, and IV dark red-brown; II red-brown (darker on sides), lightening at distal tips. Rest of I and II, light yellow patellae and tibiae striped with retrolateral sides of brown; rest of III yellow-brown, with light tarsus; rest of IV reddish-brown, with light tarsus. Tibia I ventral spination: 2–2, moderately small. Legs lightly hirsute.

Pedipalp with a very short tibial apophysis. Tarsus with globose genital bulb drawn out into a long neck with a straight, moderately short embolus with a clear twist at the end (Fig. 176, 177).

Diagnosis. Castianeira zembla differs from other *dubia* group species in its elongated abdomen (abdomen index 30) and in its genitalia (embolus very distinct from rest of genital bulb).

Remarks. This species is closely related to *C. dubia* and is probably an ant mimic.

Natural history. Nothing is known of the habits of this species.

Distribution. Known only from its type locality in Chiapas, Mexico (Map 10).

Records. MEXICO. *Chiapas.*

Castianeira rica new species

Figures 162–165, 188, 189. Map 10.

Holotype. Male from Instituto Interamericano Ciencias Agricolas, Turrialba, Costa Rica, VII/VIII-1965 (J. Reiskind); in the Museum of Comparative Zoology. The specific name is from the Spanish adjective meaning rich.

MALE

Measurements. Based on holotype and 9 males; holotype listed first, range of all follows: carapace length 2.60 mm, 2.40–2.65 mm; carapace width 1.45 mm, 1.40–1.50 mm; carapace index 56, 55–57; sternum length 1.30 mm, 1.20–1.30 mm; sternum width 0.85 mm, 0.80–0.90 mm; sternum index 65, 65–68.

Femur IV length 2.50 mm, 2.30–2.55 mm;

femur IV width 0.45 mm, 0.35–0.45 mm; leg thickness index 18, 15–19; leg length index 95, 88–96.

Abdomen length 3.30 mm, 3.20–3.60 mm; abdomen width 1.10 mm, 1.10–1.30 mm; abdomen index 34, 33–38.

Embolus length 0.10 mm, 0.08–0.11 mm; bulb length 0.82 mm, 0.78–0.85 mm; male genital index 12, 10–14.

Description. Carapace orange, with some short, dark hairs on thoracic region and longer white hairs on cephalic region. Head narrow (cephalic width index 55–57) and smoothly truncated anteriorly. Eyes moderate, equal (except anterior lateral eyes smaller than the rest), and bordered in brown-black. Thoracic groove moderate.

Abdomen an elongate cylinder moderately constricted in middle, with a full dorsal sclerite, red-brown at anterior with yellow hairs, bright orange at constriction with whitish hairs, followed by a band of dark hair, and the posterior third with yellow hair on orange-brown sclerite base (Fig. 188). Dark reddish brown epigastric sclerite, long ventral sclerite from red-brown (anterior) to yellow-orange (posterior). Very small orange-brown inframammilliary sclerite. First pair of abdominal setae very thin and very long, second pair very thin but only moderately long.

Sternum shield-shaped and yellow, with a few long, thin setae.

Chelicerae dark yellow, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth; with a very small denticle just medial and distal to the larger promargin tooth.

Coxae I–III white, coxa IV light yellow. Trochanter IV notch moderately small.

Femora I and II yellow, III yellow-orange, all with lateral sides slightly darker. All tarsi cream colored. Rest of I and II very light yellow; rest of III yellow-orange; all of IV orange-brown. Tibia I ventral spination: 3–2, thin (proximal prolateral spine smaller than rest). Legs lightly hirsute.

Pedipalp with a blunt, short, tibial apophysis. Tarsus with globose genital bulb drawn out into a long neck with a straight moderately short embolus with a distinct twist at the tip (Figs. 164, 165).

FEMALE

Measurements. Based on 10 females: carapace length 2.95–3.30 mm; carapace width 1.65–1.90 mm; carapace index 57–59; sternum length 1.40–1.60 mm; sternum width 0.95–1.10 mm; sternum index 68–73.

Femur IV length 2.20–2.40 mm; femur IV width 0.50–0.55 mm; leg thickness index 22–23; leg length index 72–76.

Abdomen length 2.85–3.85 mm; abdomen width 1.40–2.35 mm; abdomen index 46–64; dorsal sclerite length 1.30–1.50 mm; dorsal sclerite width 0.95–1.15 mm; dorsal sclerite index 68–77.

Description. Carapace red-brown (slightly lighter in cephalic region), with sparse, short, white hairs, longer on cephalic region. Head narrow (cephalic width index 57–59) and smoothly truncated anteriorly. Eyes moderately large and all equal, except the anterior lateral eyes almost half the size of the other eyes. Thoracic groove moderate.

Abdomen a wide oval, with a moderately large, red-brown, anterior dorsal sclerite and faint light horizontal hair stripes—two wide bands over the sclerite followed by a pair of spots and a thin median band. The brownish black abdomen with some horizontal light pigmentation bands on posterior half (Fig. 189). Dark red-brown epigastric sclerite and small red-brown inframammilliary sclerite. Ventrum with a longitudinal white bar and two horizontal oval white spots on each side just above mid-line. Both pairs of abdominal setae very thin and long.

Sternum shield-shaped, yellow-orange, with very sparse, thin setae.

Chelicerae orange-brown, with two mod-

erate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth; with a very small denticle just medial and distal to the larger promargin tooth.

Coxa I brownish white, II and III cream white, IV yellow-brown. Trochanter IV notch fairly small.

Femur I dark brown, femur II deep yellow with brown lateral sides, femora III and IV orange-brown, darker on lateral sides. Patella-tibia I yellow-white, rest of I yellow-brown; patella-tibia II light yellow, rest of II deep yellow; rest of III deep yellow-orange; patella-tibia IV from light red-brown proximally to red-brown distally, metatarsus IV light red-brown, tarsus IV light yellow-brown. Tibia I ventral spination: 3–2, with moderately long and thin spines. Legs moderately hirsute.

External epigynum with widely separated, moderately large circular openings (Fig. 162). Internal structure with globose spermathecae narrowing to fairly thin posterior necks (Fig. 161).

Diagnosis. Males of *Castianeira rica* differ from other *dubia* group species in their bright orange color. The females have a distinct abdominal pattern.

Remarks. Castianeira rica is an ant-mimicking spider exhibiting strong sexual dimorphism.

Natural history. This species is found on dead leaves in shady areas. It walks with an ant-like gait; the first pair of legs is raised, giving an illusion of antennae. The reddish male appears to mimic reddish ectatommine or attine ants, whereas the darker female mimics darker and slightly larger ponerines.

C. rica makes a slightly oval, disclike, white egg case on the underside of dead leaves. Of seven egg cases studied, one had seven eggs, two had eight eggs, two had nine eggs, and one had ten eggs (an average of 8.6 eggs per case).

Distribution. Southern Mexico to Costa Rica (Map 10).

Records. MEXICO. *Chiapas.* COSTA RICA. Turrialba.

The *alba* Group

Castianeira alba new species

Figures 143, 144, 157, 158, 160, 161. Map 10.

Holotype. Female from the Instituto Interamericana Ciencias Agricolas, Turrialba, Costa Rica, VII/VIII-1965 (J. Reiskind); in the Museum of Comparative Zoology. The specific name is an adjective meaning white.

MALE

Measurements. Based on 8 males: carapace length 2.75–3.25 mm; carapace width 1.95–2.25 mm; carapace index 69–72; sternum length 1.25–1.45 mm; sternum width 1.05–1.25 mm; sternum index 81–88.

Femur IV length 2.20–2.55 mm; femur IV width 0.65–0.75 mm; leg thickness index 29–31; leg length index 78–81.

Abdomen length 3.15–3.70 mm; abdomen width 1.70–1.95 mm; abdomen index 52–58.

Embolus length 0.16–0.21 mm; bulb length 0.98–1.16 mm; male genital index 16–18.

Description. Carapace maroon-brown, with short white hairs in a wide longitudinal band, with two wide lateral bands (hairs longer in cephalic region), and between the bands two longitudinal bands of black hair. Head narrow (cephalic width index 47–50) and smoothly truncated anteriorly. Eyes moderate and all about equal, except anterior lateral eyes smaller than the rest. Thoracic groove moderately strong.

Abdomen a long oval, with a full, dark maroon, dorsal sclerite covered with black and white hairs—white hair pattern with two wide horizontal white hair bands at anterior end followed by two white spots, then a medial white hair band split medially and attached to the preceding spots, then followed by a pair of small spots and

three narrow horizontal bands (Fig. 157). Epigastric, full ventral and moderate inframammilliary sclerites maroon with dark hairs. First pair of abdominal setae very thin and long, second pair moderately thin and shorter.

Sternum red-brown with very sparse, thin setae.

Chelicerae red-brown, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller then the retromargin teeth; a very small denticle just medial and distal to the larger promargin tooth.

Coxae light orange-brown (hind ones darker). Trochanter IV notch moderate.

Femora I and II orange-brown, III and IV dark red-brown. Rest of legs I and II from yellow-orange proximally to light yellow distally; rest of leg III from red-brown to yellow; rest of leg IV dark maroon-brown patella-tibia and metatarsus and yellow-brown tarsus. Legs heavily hirsute with abundant black and white hairs on femora and white hairs at both ends of tibia IV. Tibia I ventral spination: 3–2, moderately thick and short.

Pedipalp with a blunt, almost negligible, tibial apophysis. Tarsus with a globose genital bulb drawn out into a long neck with a stout, straight embolus and a terminal twist (Figs. 143, 144).

FEMALE

Measurements. Based on holotype and 5 females, holotype listed first, range of all follows: carapace length 3.70 mm, 3.25–3.75 mm; carapace width 2.55 mm, 2.45–2.75 mm; carapace index 69, 69–75; sternum length 1.65 mm, 1.60–1.75 mm; sternum width 1.35 mm, 1.30–1.40 mm; sternum index 82, 80–82.

Femur IV length 2.65 mm, 2.50–2.80 mm; femur IV width 0.80 mm, 0.75–0.90 mm; leg thickness index 30, 30–32; leg length index 72, 72–76.

Abdomen length 4.20 mm, 4.20–4.40 mm; abdomen width 2.65 mm, 2.65–2.75 mm; abdomen index 63, 62–63; dorsal sclerite length 1.30 mm, 1.15–1.40 mm; dorsal sclerite width 1.00 mm, 0.95–1.10 mm; dorsal sclerite index 76, 76–83.

Description. Carapace dark maroon-brown, with short white hairs in a wide longitudinal band, with two wide lateral bands (hairs longer in cephalic region), and between these bands two longitudinal bands of black hair. Head narrow (cephalic width index 52–57) and smoothly truncated anteriorly. Eyes moderate and all about equal, except anterior lateral eyes much smaller than the rest. Thoracic groove moderately strong.

Abdomen a wide oval, with a moderately small, maroon dorsal sclerite and covered with black and white hairs—two wide horizontal white hair bands at anterior end followed by a pair of white spots, then a white hair band split medially, then finally by a series of about six thin white hair bands (sometimes pairs of spots) (Fig. 158). Epigastric sclerite red-brown. Ventrum with a pair of parallel light stripes down the center, a pair of white hair spots on each side. A small maroon inframammilliary sclerite. Both pairs of abdominal setae thin and long.

Sternum shield-shaped, red-brown, with moderately thin, sparse setae.

Chelicerae dark red-brown, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth; with a very small denticle just medial and distal to the larger promargin tooth.

Coxae all brown. Trochanter IV notch moderate.

Femora all red-brown, hind femora much darker. Rest of legs I and II yellow-brown; rest of leg III fairly dark red-brown, with yellow-brown tarsus; rest of leg IV dark red-brown, with a yellow-brown tarsus. Legs heavily hirsute, with black and white hairs abundant on femora and at both ends of tibia IV. Tibia I ventral spination: 3–2, moderate.

External epigynum with two fairly small, high openings (Fig. 161). Internal structure with globose spermathecae extended with thick necks posteriorly (Fig. 160).

Diagnosis. The anterior median eyes of *Castianeira alba* are larger than the laterals, the carapace is very wide (carapace index 69–75), and the abdominal pattern is distinct, distinguishing it from all other *Castianeira.*

Remarks. This species has the eye arrangement of the *dubia* group, but the female genitalia and body proportions are radically different. The latter characters are probably the result of *C. alba*'s non-mimetic habits.

Natural history. This species is found on dead leaves and sticks in sunlit areas. Usually it rests under the edge of a leaf; it runs, never walks, from under one leaf to under another. Sometimes this spider suns itself for up to about 30 seconds, pumping its abdomen up and down in the same manner as *Castianeira variata.*

C. alba makes an almost round, white, disclike egg sac on the undersides of dry, dead leaves. Of four egg sacs studied, one had 12 eggs, one had 17, and two had 14 (an average of 16.3 eggs per case).

Distribution. Costa Rica to Panama (Map 10).

Records. COSTA RICA. Turrialba.

PANAMA. Boquete.

CANAL ZONE. Barro Colorado Island, Chilibre, Fort Sherman, France Field, Summit.

THE *SIMILIS* GROUP

Castianeira similis (Banks), new combination Figures 166, 167, 184–186. Map 11.

Myrmecotypus similis Banks, 1929, Bull. Mus. Comp. Zool. 69:61, fig. 70, "♀." Penultimate female holotype from Barro Colorado Island, Panama Canal Zone; in the Museum of Comparative Zoology, examined.

FEMALE

Measurements. Based on 2 females: carapace length 4.15–5.10 mm; carapace width 2.30–2.75 mm; carapace index 54–56; sternum length 1.95–2.35 mm; sternum width 1.15–1.45 mm; sternum index 59–62.

Femur IV length 3.05–3.75 mm; femur IV width 0.65–0.70 mm; leg thickness index 19–21; leg length index 74.

Abdomen length 5.45–6.10 mm; abdomen width 2.05–2.45 mm; abdomen index 37–40; dorsal sclerite length 1.70–2.10 mm; dorsal sclerite width 1.10–1.30 mm; dorsal sclerite index 63–66.

Description. Carapace deep maroon-black, punctate, surface with long white hairs on head region. Head region distinguished from the thorax region by a slight impression reinforced with black hairs. Head narrows (cephalic width index 65–67) and is distinctly truncated anteriorly (Fig. 186). Eyes equal, except anterior median eyes almost twice as large as anterior lateral eyes. Thoracic groove strong.

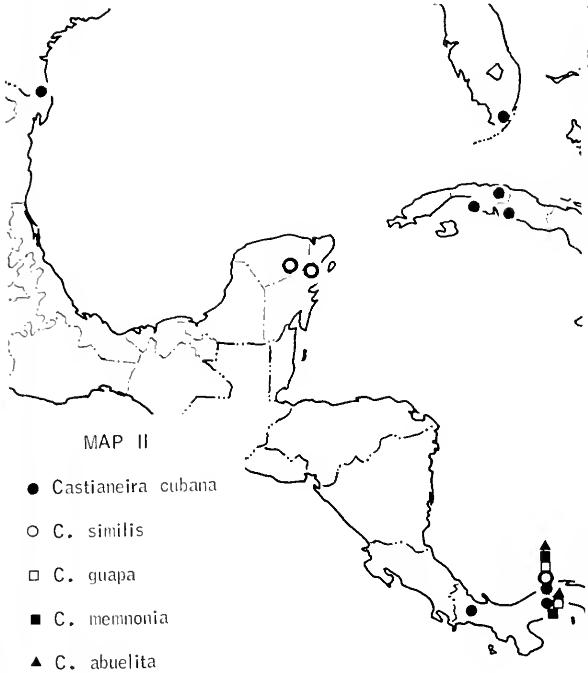
Abdomen elongated and ponerine-like, with a fairly small, red-brown, dorsal sclerite and a slight median constriction (Figs. 184, 185). Several horizontal bands of blackish hairs and many very long, thin setae. Epigastric sclerite red-brown. Ventrum with a lighter elongated area constricted in middle, with a small, red-brown inframammilliary sclerite.

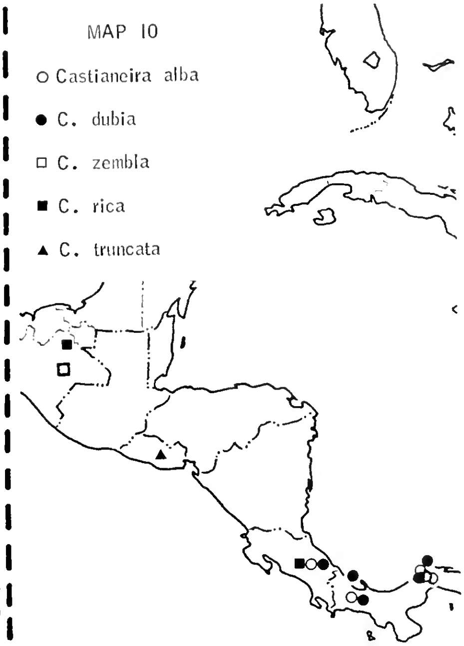
Sternum long, shield-shaped, dark red-brown, and covered with fine setae. Pedicel short.

Chelicerae dark red-brown, with two moderately large retromargin teeth, the distal one slightly larger, and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin; with a small denticle just medial and distal to the larger promargin tooth.

Coxae I–III bright white; coxa IV with basal half red-brown, distal half bright white. Trochanter IV notch small.

Femora I and II, proximal two-thirds red-brown, distal one-third white; femora III and IV red-brown. Rest of I and II with strongly striped patellae and tibiae





(lateral and dorsal stripes of dark brown on white), metatarsus I dark maroon-brown, metatarsus II red-brown, tarsus I yellow, tarsus II yellow-brown; rest of III dark red-brown, except yellow-brown tarsus; rest of IV dark red-brown. Tibia I ventral spination: 3–3, strong and long. Legs lightly hirsute but fairly heavily spiney.

External epigynum with two round openings (Fig. 167). Internal structure with rounded, saclike spermathecae and short, thick posterior necks (Fig. 166).

Diagnosis. This very large species (carapace length 4.15–5.10 mm) has a wide cephalic region, thin legs (leg thickness index 19–21), and long, simple hairs on posterior of abdomen.

Remarks. *Castianeira similis* was described by Banks (1929) from an immature female whose non-genitalic characters closely match those of two mature females from Yucatan. It is not closely related to *Castianeira salticina* Taczanowski, as Banks (1929) claimed.

The species has a ponerine-like abdomen (Fig. 184), most dramatic when viewed laterally, the spinnerets placed where the sting is located in a ponerine ant.

Natural history. Nothing is known of the habits of this species, but it is undoubtedly a ponerine ant mimic.

Distribution. Yucatan, Panama, probably Central America (Map 11).

Records. MEXICO. *Quintana Roo, Yucatan.*

CANAL ZONE. Barro Colorado Island.

THE *MEMNONIA* GROUP

Castianeira memnonia (C. L. Koch)
Figures 178–181, 194–196. Map 11.

Corinna memnonia C. L. Koch, 1842, Die Arachniden 9:20–21, fig. 704, ♀, from Colombia (included Panama before 1903); lost.

Thargalia memnonia: Karsch, 1880, Z. Ges. Naturwiss. 53:376.

Castaneira memnonia: Simon, 1897, Histoire Naturelles des Araignées 2(1):167.

Castianeira memnonia: Banks, 1929, Bull. Mus. Comp. Zool. 69(3):59, pl. 1, fig. 11, pl. 3, fig. 50, pl. 4, fig. 64, ♂, ♀. Chickering, 1937, Trans. Amer. Microscop. Soc. 56(1):4, figs. 44, 61, ♂.

MALE

Measurements. Based on 9 males: carapace length 2.50–3.05 mm; carapace width 1.40–1.70 mm; carapace index 55–58; sternum length 1.15–1.40 mm; sternum width 0.75–0.95 mm; sternum index 64–71.

Femur IV length 2.60–3.20 mm; femur IV width 0.40–0.50 mm; leg thickness index 15–17; leg length index 94–110.

Abdomen length 3.05–3.90 mm; abdomen width 1.15–1.45 mm; abdomen index 36–41.

Description. Carapace orange-brown, with some white hairs, longer in cephalic region. Head narrow (cephalic width index 51–55) and smoothly truncated anteriorly (Fig. 180). Eyes raised—posterior eyes large and equal, anterior median eyes very much larger, anterior lateral eyes much smaller (Fig. 179). Thoracic groove moderate.

Abdomen elongated, with a smooth, median constriction, with a full red-brown sclerite, anterior half darker than the posterior half, with some white hairs in a horizontal band at the constriction (Fig. 181). Epigastric sclerite red-brown. Narrow, orange-brown ventral sclerite and a small, orange-brown inframammilliary sclerite. First pair of abdominal setae very thin, second pair thin, both pair long.

Sternum shield-shaped, long, orange-brown, with some short, very fine, sparse hairs and several thin setae.

Chelicerae light-brown, with two moderately large retromargin teeth and three promargin teeth, the median larger, the proximal smaller, and the distal very much smaller than the retromargin teeth.

Coxae all cream white. Trochanter IV notch small.

Femora I–III striped with brown sides and yellow-brown ventrally and dorsally (lighter distally and darker on leg III), femur IV dark red-brown, slightly striped; rest of legs I and II light yellow-brown (except metatrasus I, brown); rest of leg III with patella, tibia, and metatarsus striped (lateral sides brown) and tarsus yellow-brown; rest of leg IV red-brown, except a yellow-brown tarsus. Legs lightly hirsute. Tibia I ventral spination: 3–3, moderately small.

Pedipalp with a heavy, blunt, tibial apophysis. Tarsus with a large globose bulb drawn into a short thick neck and a doubly hooked terminal sclerotized section, the tip of the cymbium curved ventrally (Fig. 196).

(This is a fairly lightly pigmented specimen.)

FEMALE

Measurements. Based on 8 females: carapace length 2.95–3.50 mm; carapace width 1.65–1.95 mm; carapace index 55–57; sternum length 1.30–1.65 mm; sternum width 0.95–1.10 mm; sternum index 65–73.

Femur IV length 3.05–3.75 mm; femur IV width 0.45–0.60 mm; leg thickness index 15–17; leg length index 102–108.

Abdomen length 4.00–5.40 mm; abdomen width 1.65–2.50 mm; abdomen index 33–62; dorsal sclerite length 1.10–1.50 mm; dorsal sclerite width 0.60–0.80 mm; dorsal sclerite index 48–60.

Description. Carapace dark reddish-brown, elongated, with short whitish hairs, longer hair on cephalic region. Head narrow (cephalic width index 57–62) and smoothly truncated anteriorly. Eyes raised —posterior eyes large and equal, anterior median eyes very much larger, anterior lateral eyes much smaller. Thoracic groove moderately weak.

Abdomen elongated, slightly constricted in middle, with a very dark, red-brown, elongated, moderately small dorsal sclerite. Three horizontal bands of white hairs—one at posterior edge of sclerite, one at constriction, and one near posterior end; rest of dorsum with brownish hairs (Fig. 178). Epigastric sclerite dark red-brown. Two thin light stripes from sides of epigastric furrow to area just anterior to the

spinnerets. First pair of abdominal setae very thin and long, second pair thin and long.

Sternum shield-shaped, long, and very dark red-brown, with some short, very fine, sparse hairs.

Chelicerae very dark red-brown, with two moderately large retromargin teeth and three promargin teeth, the median larger, the proximal smaller, and the distal much smaller than the retromargin teeth.

Coxa I brown, coxae II–IV light yellow-white. Trochanter IV notch very small.

Femora deep maroon-brown, distal ends of femora I and II slightly striped; rest of legs I and II with patella-tibia yellow (sides of patella darker), metatarsi yellow-brown, tarsi yellow (leg II darker); rest of legs III and IV dark red-brown, with tarsi yellow-brown. Legs fairly lightly hirsute. Tibia I ventral spination: 3–3, long and moderately thin.

External epigynum two thin horizontal slits (Fig. 195). Internal structure with a large saclike spermathecae with two small, twisted, posterior extensions (Fig. 194).

Diagnosis. Castianeira memnonia differs from all other *Castianeira* in its genitalia.

Remarks. Of all the Castianeirinae in North and Central America, this species comes closest to that of the type-species, *Castianeira rubicunda,* with its male genitalia having the same type of twisted end as in the type-species. *C. memnonia* is probably a generalized ponerine ant mimic.

Natural history. Nothing is known of the habits of this species.

Distribution. Panama (Map 11).

Records. CANAL ZONE. Barro Colorado Island, Diablo, Forest Reserve.

THE *CUBANA* GROUP

Characteristics. Small (male carapace length 1.65–2.15 mm; female carapace length 1.75–2.40 mm), with a carapace index 57–63. Cephalic region fairly wide (cephalic width index 60–73) and the carapace high and rounded. Eyes equal or anterior median eyes larger than anterior lateral eyes. Thoracic groove weak. Female epigyna with fairly wide, slightly twisted spermathecal necks.

Discussion. This group includes the very *Myrmecotypus*-like *C. cubana* (Banks) and two other species. The presence of the thoracic groove and the eye arrangements clearly place the group in the *Castianeira.*

Castianeira cubana (Banks), new combination. Figures 216–219, 276. Map 11.

Myrmecotypus cubanus Banks, 1926, Trans. *Entomol.* Soc. London 74:433–434, fig. 1, pl. 93, fig. 2, ♂, imm. ♀. Male holotype from Soledad, Cuba; in the Museum of Comparative Zoology, examined.

MALE

Measurements. Based on holotype and 7 males, holotype listed first, range of all follows: carapace length 1.75 mm, 1.65–1.95 mm; carapace width 1.10 mm, 1.00–1.15 mm; carapace index 64, 58–64; sternum length 0.75 mm, 0.70–0.75 mm; sternum width 0.65 mm, 0.60–0.65 mm; sternum index 83, 78–86.

Femur IV length 1.20 mm, 1.05–1.30 mm; femur IV width 0.30 mm, 0.30–0.40 mm; leg thickness index 24, 24–33; leg length index 69, 64–69.

Abdomen length 1.70 mm, 1.70–2.05 mm; abdomen width 1.20 mm, 0.95–1.25 mm; abdomen index 72, 54–73.

Embolus length 0.07 mm, 0.06–0.07 mm; bulb length 0.60 mm, 0.56–0.60 mm; male genital index 11, 10–12.

Description. Carapace orange-brown and hairless. Eyes fairly small and equal, except the anterior median eyes almost twice the diameter of anterior laterals, anterior row recurved and posterior row almost straight when viewed dorsally, the posterior row about one-fifth wider than the anterior row. Carapace somewhat narrow in cephalic region (cephalic width index 66–70) and roundly truncated anteriorly. Thoracic groove weak.

Abdomen short and drop-like, with an

almost full, dark brown dorsal sclerite and light pubescence (Fig. 276). Ventral abdomen with a dark orange-brown epigastric sclerite, and rectangular, red-brown ventral sclerite. Both pairs of abdominal setae very thin. No petiole, and pedicel very short.

Sternum dark orange-brown and fairly wide and shield-like, with no setae.

Chelicerae light orange-brown, with two moderate retromargin teeth and two promargin teeth, the distal one much larger and the proximal one slightly smaller than the retromargin teeth. A small, distinct denticle just distal and slightly median to the larger promargin tooth.

Coxa I brown, coxae II, III, and IV white. Trochanter IV notch small.

Legs red-brown, all femora and legs III and IV darker, rest of legs I and II lighter. Legs moderately hirsute. Tibia I ventral spination: 3–2, small.

Pedipalp with no tibial apophysis. Tarsus with a globose genital bulb drawn out into a long neck with a short, straight embolus. Distinctive looping in genital bulb (Figs. 218, 219).

FEMALE

Measurements. Based on 8 females: carapace length 1.75–2.05 mm; carapace width 1.05–1.20 mm; carapace index 58–63; sternum length 0.70–0.85 mm; sternum width 0.55–0.70 mm; sternum index 77–87.

Femur IV length 1.10–1.40 mm; femur IV width 0.30–0.35 mm; leg thickness index 23–31; leg length index 63–70.

Abdomen length 1.85–2.20 mm; abdomen width 1.30–1.85 mm; abdomen index 67–88; dorsal sclerite length 1.35–1.85 mm; dorsal sclerite width 1.30–1.60 mm; dorsal sclerite index 75–119.

Description. Carapace orange-brown and hairless. Eyes fairly small and equal, except the anterior median eyes almost twice the diameter of the anterior laterals, anterior row recurved and posterior row almost straight when viewed dorsally. Carapace somewhat narrow in cephalic region (cephalic width index 64–73) and roundly truncated anteriorly. Thoracic groove weak.

Abdomen short and wide, with a large, dark red-brown dorsal sclerite; some light hairs on sclerite and dark gray-brown abdomen. Ventrum gray-brown. Both pairs of abdominal setae very thin. No petiole, pedicel very short.

Sternum shield-shaped, red-brown, with some thin hairs.

Chelicerae light orange-brown with two moderate retromargin teeth and two promargin teeth, the distal one much larger and the proximal one slightly smaller than the retromargin teeth. A small distinct denticle just distal and slightly median to the larger promargin tooth.

Coxa I brown, coxae II–IV white. Trochanter IV notch small.

Femur I red-brown, lightening to yellow distally, femora II–IV striped—dorsal, pro- and retrolateral brown striped on yellow (darker yellow in IV)—the yellow areas reinforced by light hairs. Rest of legs I and II with patellae, tibiae, and metatarsi striped—brown sides on light yellow; tarsi light yellow. Rest of III, patella-tibia red-brown (slightly striped), metatarsus red-brown, tarsus yellow-orange. Rest of leg IV, red-brown patella-tibia, dark red-brown metatarsus, orange tarsus. Legs moderately hirsute. Tibia I ventral spination: 3–2, moderately small.

External epigynum with two small, semicircular openings directed medially (Fig. 216). Internal structure with rounded sac-like spermathecae narrower at posterior ends (Fig. 217).

Diagnosis. C. cubana differs from other species in the *cubana* group in its single-colored carapace, its large anterior median eyes, and its male genitalia (male genital index 10–12), which has an extra loop in the main palpal duct (Fig. 218).

Remarks. Two distinct color forms of this species exist: a Cuban-Texan-Floridian form, with an orange to red-brown carapace and a brown coxa I, and a Panamanian

form, with a deep brown-black carapace and white coxa I. The two forms have similar dimensions and genitalia.

Natural history. Castianeira cubana (Banks) is a mimic of *Camponotus planatus* Roger, resembling the ant both in color and gait—the first pair of legs moving "in a manner at once suggestive of the movements of an ant's antennae" (Myers and Salt, 1926).

Distribution. Cuba, Texas, Florida, and Panama (Map 11).

Records. Florida. Dade Co. *Texas.* Cameron Co.

CUBA. Cienaga de Zapata, Soledad.

PANAMA. Arraijan, Boquete.

CANAL ZONE. Barro Colorado Island, Experimental Gardens, Summit.

Castianeira guapa new species

Figures 212–215, 277, 278. Map 11.

Holotype. Male from Summit, Panama Canal Zone, 23/28-VIII-1950 (A. M. Chickering); in the Museum of Comparative Zoology. The specific name is the Spanish word for handsome.

MALE

Measurements. Based on holotype and 3 males, holotype listed first, range of all follows: carapace length 2.05 mm, 1.80–2.15 mm; carapace width 1.20 mm, 1.05–1.20 mm; carapace index 59, 57–59; sternum length 0.95 mm, 0.85–0.95 mm; sternum width 0.65 mm, 0.60–0.70 mm; sternum index 68, 68–74.

Femur IV length 1.55 mm, 1.30–1.60 mm; femur IV width 0.40 mm, 0.30–0.40 mm; leg thickness index 27, 24–27; leg length index 75, 71–75.

Abdomen length 2.25 mm, 1.90–2.25 mm; abdomen width 1.30 mm, 1.10–1.30 mm; abdomen index 57, 55–58.

Embolus length 0.13 mm, 0.11–0.13 mm; bulb length 0.70 mm, 0.61–0.70 mm; male genital index 19, 18–19.

Description. Carapace with yellow-orange cephalic region, dark brown thoracic region covered with white hairs, and long white hairs on cephalic region. Eyes moderately small, posterior eyes equal, anterior median eyes somewhat larger and anterior lateral eyes smaller than the posterior eyes. Eyes bordered in black. Carapace narrowed in cephalic region (cephalic width index 58–64) and roundly truncated anteriorly. Thoracic groove weak.

Abdomen a droplike oval (widening posteriorly), with an almost full, dark red-brown dorsal sclerite with three horizontal bands of white—a narrow one near anterior end, wide median and posterior bands (the latter of long hairs). Epigastric sclerite dark red-brown, ventral sclerite (almost full) and small inframammilliary sclerite red-brown. Both pairs of abdominal setae very thin and long.

Sternum shield-shaped, orange-brown with some dark patches opposite the posterior coxae, with thin, light hairs.

Chelicerae light yellow-orange, with two moderately small retromargin teeth and two promargin teeth, the distal one larger, the proximal smaller than the retromargin teeth. Slight trace of a denticle median and distal to larger promargin tooth.

Coxa I light brown, coxae II–IV yellow-white (IV slightly darker). Trochanter IV notch small.

Femora I and II light brown lightening to yellow-white at distal end, femora III and IV dark brown with pairs of yellow with white hair stripes on both sides of femoral dorsa. Rest of legs I and II yellow-white, rest of leg III with striped patella-tibia (dark brown sides and dorsum), yellow-brown metatarsus, yellow-white tarsus, rest of leg IV with striped patella-tibia—dark brown with a single dorsal-retrolateral, yellow-white stripe—dark red-brown metatarsus and tarsus with a dark brown base and yellow-white distal half, Legs moderately hirsute. Tibia I ventral spination: 3–2, small and weak (proximal ones smaller).

Pedipalp with a moderate, blunt, tibial

apophysis. Tarsus with a globose genital bulb drawn out into a long neck with a curved, fairly long embolus, clubbed at tip (Figs. 214, 215).

FEMALE

Measurements. Based on 2 females: carapace length 2.25–2.40 mm; carapace width 1.35–1.40 mm; carapace index 58–59; sternum length 1.00–1.05 mm; sternum width 0.75 mm; sternum index 75.

Femur IV length 1.65–1.75 mm; femur IV width 0.40 mm; leg thickness index 24; leg length index 73–74.

Abdomen length 2.60–2.85 mm; abdomen width 1.65–1.75 mm; abdomen index 61–63; dorsal sclerite length 0.90–0.95 mm; dorsal sclerite width 0.85 mm; dorsal sclerite index 87–93.

Description. Carapace with a bright yellow-orange cephalic region, dark brown thoracic region covered with some white hairs (Fig. 278). Eyes moderately small, posterior eyes equal, anterior median eyes somewhat larger and anterior lateral eyes smaller than the posterior eyes. Eyes bordered in black. Carapace narrowed in cephalic region (cephalic width index 63–66) and roundly truncated anteriorly. Thoracic groove extremely weak.

Abdomen droplike oval, with a moderate, dark red-brown dorsal sclerite and three horizontal bands of white hairs—a narrow one over the sclerite, and broad median and posterior bands over a purple-brown ground (Fig. 277). Red-brown epigastric and small inframammilliary sclerites. Ventrum with a pair of light lines from each side of epigastric furrow to the posterior sclerite. First pair of abdominal setae very thin and long, second pair thin and long.

Sternum shield-shaped, orange-brown, with some dark patches opposite the posterior coxae, with thin, light hairs and a few long setae.

Chelicerae yellow, with two moderately small retromargin teeth and two promargin teeth, the distal one larger, the proximal smaller than the retromargin teeth. Slight trace of a denticle median and distal to larger promargin tooth.

Coxa I brown, coxae II–IV creamy-white. Trochanter IV notch small.

Femora I and II light-brown lightening to yellow-white at distal end, femora III and IV dark brown with pairs of yellow with white hair stripes on both sides of femoral dorsa. Rest of legs I and II yellow-white; rest of leg III with striped patella-tibia (dark brown sides and dorsum), yellow-brown metatarsus, yellow-white tarsus; rest of leg IV with striped patella-tibia—dark brown with a single dorsal-retrolateral yellow-white stripe—dark red-brown metatarsus and tarsus with a dark brown base and yellow-white distal half. Legs moderately hirsute. Tibia I ventral spination: 3–2, moderate.

External epigynum with two very small, semicircular openings directed medially (Fig. 213). Internal structure with bag-like spermathecae with twisted necks (Fig. 212).

Diagnosis. *Castianeira guapa* differs from all other *cubana* group species in its bicolored carapace (cephalic region much lighter) and its distinctive embolus on the male pedipalp.

Remarks. This is the least *Myrmecotypus*-like of the three species in the *cubana* group, with eyes approximately equal and a moderately small dorsal abdominal sclerite.

Natural history. Nothing is known of the habits of this species.

Distribution. Panama (Map 11).

Records. CANAL ZONE. Balboa, Barro Colorado Island, Corozal, Fort Clayton, Summit.

Castianeira abuelita new species
Figures 220, 221, 279. Map 11.

Holotype. Female from Barro Colorado Island, Panama Canal Zone, 30-VII-1954

(A. M. Chickering); in the Museum of Comparative Zoology. The specific name is from the Spanish noun meaning "grandma."

FEMALE

Measurements. Based on holotype and 3 females, holotype listed first, range of all follows: carapace length 2.25 mm, 2.25–2.30 mm; carapace width 1.40 mm, 1.40–1.45 mm; carapace index 63, 62–63; sternum length 1.05 mm, 1.05 mm; sternum width 0.80 mm, 0.80–0.85 mm; sternum index 77, 77–81.

Femur IV length 1.60 mm, 1.55–1.65 mm; femur IV width 0.50 mm, 0.45–0.50 mm; leg thickness index 32, 30–32; leg length index 70, 69–71.

Abdomen length 2.65 mm, 2.55–2.90 mm; abdomen width 1.60 mm, 1.55–1.75 mm; abdomen index 60, 60–61; dorsal sclerite length 1.55 mm, 1.35–1.65 mm; dorsal sclerite width 1.20 mm, 1.20–1.30 mm; dorsal sclerite index 79, 79–95.

Description. Carapace dark red-brown, vaulted high, with white hairs, longer in cephalic region. Eyes moderate, equal, and bordered in black. Carapace narrow in cephalic region (cephalic width index 60–63) and roundly truncated anteriorly. Thoracic groove small.

Abdomen oval, with a moderately large, red-brown dorsal sclerite (over one-half length of abdomen), and with a complex pattern of white and dark hairs—predominantly white hairs, with several complete and incomplete bands of dark hairs—a major wide dark band just posterior to the sclerite. Epigastric and very small inframammilliary sclerites red-brown. Ventrum covered with white hairs. First pair of abdominal setae very thin and long, second pair thin and shorter.

Sternum shield-shaped, red-brown, and covered with light, long hairs.

Chelicerae dark red-brown, with two moderately small retromargin teeth and two promargin teeth, the distal larger and the proximal smaller than the retromargin teeth. No denticle present.

Coxa I brown, coxae II–IV yellow-white. Trochanter IV notch moderate.

Femora I and II dark brown lightening to yellow-white distally; femur III striped—dark brown sides, yellow dorsum and ventrum (with white hairs on dorsum); femur IV deep red-brown, with some white hairs with a light yellow distal tip. Rest of legs I and II yellow-white; rest of leg III yellow with dark brown on both sides of patella and retrolateral side of tibia and metatarsus; rest of leg IV patella-tibia and metatarsus deep red-brown, with proximal end of patella and distal end of tibia yellow, the latter with heavy white hairs, white hair striping on tibia and metatarsus, tarsus yellow. Legs moderately hirsute. Tibia I ventral spination: 2–1, moderate.

External epigynum with two semicircular, small openings, opening laterally (Fig. 221). Internal structure with somewhat globose spermathecae narrowing to twisted necks (Fig. 220).

Diagnosis. C. abuelita differs from other *cubana* group species in the white hairs on the carapace and the hair pattern on the abdomen (Fig. 279). Also, the epigynal openings are small and directed laterally (Fig. 221).

Remarks. This species is intermediate in dorsal abdominal sclerite size and eye sizes between *C. cubana* and *C. guapa.*

Natural history. Nothing is known of the habits of this species.

Distribution. Panama (Map 11).

Records. CANAL ZONE. Barro Colorado Island, Chilibre, France Field.

The *peregrina* Group

Castianeira peregrina (Gertsch)
Figure 207. Map 12.

Mazax peregrina Gertsch, 1935, Amer. Mus. Novit. No. 805:5, fig. 30, ♀, from 5 miles S. San Juan, Texas; in the American Museum of Natural History, examined.

Castianeira peregrina: Gertsch and Davis, 1940, Amer. Mus. Novit. No. 1069:14.

FEMALE

Measurements. Based on holotype and one female, holotype listed first, range of both follows: carapace length 1.95 mm, 1.95–2.05 mm; carapace width 1.30 mm, 1.30–1.40 mm; carapace index 67, 67; sternum length 0.90 mm, 0.90–0.95 mm; sternum width 0.75 mm, 0.75–0.85 mm; sternum index 86, 86–87.

Femur IV length 1.40 mm, 1.40–1.50 mm; femur IV width 0.35 mm, 0.35–0.40 mm; leg thickness index 26, 24–26; leg length index 72, 72–73.

Abdomen length 2.05 mm, 2.05–2.90 mm; abdomen width 1.25 mm, 1.25–1.75 mm; abdomen index 61, 61; dorsal sclerite length 1.05 mm, 0.95–1.05 mm; dorsal sclerite width 0.95 mm, 0.95–1.05 mm; dorsal sclerite index 88, 88–110.

Description. Carapace dark yellow, with some dark markings, and hairless. Head narrow (cephalic width index 53–58) and smoothly truncated anteriorly. Posterior eyes equal, anterior median eyes somewhat larger and anterior lateral eyes somewhat smaller. Eyes bordered in black. Thoracic groove moderately weak.

Abdomen oval, with a large, dark red-brown dorsal sclerite (over half the length of the abdomen), with a pair of white hair spots just posterior to the sclerite, rest of dorsum greyish purple. Epigastric and small inframammilliary sclerites orange-brown. Four faint parallel stripes from the epigastric furrow towards the spinnerets. First pair of abdominal setae very thin, second pair moderately thin.

Sternum shield-shaped and wide, yellow-brown, with sparse, thin setae.

Chelicerae light yellow-brown, with two moderate retromargin teeth and two promargin teeth, the distal larger and the proximal smaller than the retromargin teeth. A minute denticle just medial and distal to the larger promargin tooth.

Coxa I very light brown, coxae II–IV light yellow-white. Trochanter IV notch moderately small.

Femora I–III striped with brown on sides and rest yellow, femur IV dark yellow-brown. Rest of legs I and II light yellow-white, rest of leg III light yellow, rest of leg IV—red-brown patella-tibia, with distinct light yellow proximal end of patella and distal end of tibia, dark red-brown metatarsus, and yellow-brown tarsus. Legs lightly hirsute. Tibia I ventral spination: 2–1, small.

External epigynum with two small, highly sclerotized, semicircular openings directed laterally (Fig. 207). Internal structure with globose spermathecae extended posteriorly as outwardly curving necks.

Diagnosis. C. peregrina is a small spider with the anterior median eyes larger than the laterals, but it differs from the *cubana* group in its narrower cephalic region (cephalic width index 53–58) and from the *cincta* group in the absence of any cheliceral apical "rake" or claw.

Remarks. This species is closely related to the *cubana* group, and in its large abdominal dorsal sclerite and eye size resembles *Castianeira cubana*.

Natural history. Nothing is known of the habits of this species.

Distribution. Southern Texas (Map 12).

Records. Texas. Hidalgo Co.

The *cincta* Group

Characteristics. Very small spiders (male carapace length 1.10–1.60 mm; female carapace length 1.20–1.75 mm), with very wide carapaces (male carapace index 70–76; female carapace index 66–76) and narrow cephalic regions (male cephalic width index 47–55; female cephalic width index 51–58). A "rake" or large claw at apex of each chelicera in the females. Thoracic groove moderate to absent.

Discussion. This group includes three very distinct species whose common char-

acters are small size, wide heads, and growths at the apices of the chelicerae. These "rakes" or claws are probably adaptations to digging (like the rastellum in some mygalomorphs), though nothing is known of the habits of these spiders. For these reasons this group may well be an artificial one based on the convergence of functional characters.

Castianeira cincta (Banks), new combination Figures 190–193, 266, 267. Map 12.

Myrmecotypus cinctus Banks, 1929, Bull. Mus. Comp. Zool. 69(3):60, pl. 4, fig. 56, ♀, from Mt. Hope, Panama Canal Zone; in the Museum of Comparative Zoology, examined.

MALE

Measurements. Based on 7 males: carapace length 1.25–1.45 mm; carapace width 0.90–1.05 mm; carapace index 72–75; sternum length 0.65–0.75 mm; sternum width 0.60–0.70 mm; sternum index 88–95.

Femur IV length 0.95–1.15 mm; femur IV width 0.25–0.30 mm; leg thickness index 25–28; leg length index 75–80.

Abdomen length 1.35–1.60 mm; abdomen width 0.80–0.95 mm; abdomen index 57–61.

Embolus length 0.03–0.04 mm; bulb length 0.47–0.56 mm; male genital index 6–7.

Description. Carapace fairly wide, yellow-orange with some dark brown markings, and hairless. Eyes fairly large and almost equal, the anteriors slightly smaller than the posteriors. Head narrow (cephalic width index 52–55) and smoothly truncated anteriorly. Thoracic groove moderately weak.

Abdomen an oval with a full, orange-brown sclerite with three wide horizontal light stripes (with some white hair). Epigastric sclerite, wide rectangular ventral sclerite, and moderately large inframammilliary sclerite yellow-orange. First pair of abdominal setae very thin, second pair moderate.

Sternum mottled yellow and brown, shiny, wide, and hairless.

Chelicerae light yellow, with two moderate retromargin teeth, the distal one smaller than the proximal, and two promargin teeth, the distal one slightly larger than the larger retromargin tooth, the proximal one the same size as the distal retromargin tooth. A small denticle distal to the larger promargin tooth. Row of heavy spines at promargin side of cheliceral apex.

Coxae all cream white. Trochanter IV notch moderately small.

Femora I and II yellow; femora III and IV striped—yellow with brown lateral sides. Rest of legs I and II yellow-white; rest of leg III yellow, tibia striped like femur, tarsus yellow-white. Tibia I ventral spination: 3–2, long and moderately strong, except proximal prolateral spine moderately small.

Pedipalp with a short, sharp tibial apophysis. Tarsus with a globose genital bulb drawn out into a long neck with a very short sclerotized embolus (Figs. 192, 193).

FEMALE

Measurements. Based on holotype and 8 females, holotype listed first, range of all follows: carapace length 1.65 mm, 1.50–1.65 mm; carapace width 1.20 mm, 1.10–1.20 mm; carapace index 75, 71–75; sternum length 0.85 mm, 0.75–0.85 mm; sternum width 0.80 mm, 0.70–0.80 mm; sternum index 96, 90–96.

Femur IV length 1.40 mm, 1.20–1.40 mm; femur IV width 0.35 mm, 0.30–0.35 mm; leg thickness index 24, 24–26; leg length index 84, 78–84.

Abdomen length 2.15 mm, 1.60–2.20 mm; abdomen width 1.45 mm, 1.15–1.55 mm; abdomen index 67, 62–78; dorsal sclerite length 0.70 mm, 0.50–0.70 mm; dorsal sclerite width 0.65 mm, 0.65–0.80 mm; dorsal sclerite index 91, 91–135.

Description. Carapace fairly wide, orange-brown, and hairless. Eyes fairly large and almost equal, the anteriors (especially the anterior median eyes) slightly smaller than the posteriors; anterior row recurved, posterior row procurved when viewed dorsally, the posterior row slightly wider than the anteriors. Carapace considerably narrowed in cephalic region (cephalic width index 54–58) and roundly truncated anteriorly. Thoracic groove moderately strong.

Abdomen oval, with a small orange-brown sclerite. Rest of dorsum grey-brown with two wide, white, horizontal stripes, one over sclerite and one in middle (Fig. 266). Abdomen with light pubescence. Ventral abdomen with an orange-brown epigastric sclerite and a small orange-brown inframammilliary sclerite. First pair of abdominal setae very thin, second pair moderate and fairly short. Petiole and pedicel negligible.

Sternum orange-brown, with sparse, thin setae.

Chelicerae orange, with two moderate retromargin teeth, the distal one smaller than the proximal, and two promargin teeth, the distal one slightly larger than the larger retromargin tooth, the proximal one the same size as the distal retromargin tooth. A small denticle distal to larger promargin tooth. Row of heavy spines at promargin side of cheliceral apex (Fig. 267).

Coxae light yellow-white. Trochanter IV notch moderate.

Femora yellow-brown with red-brown sides. Rest of I and II dark yellow; rest of III light yellow-brown; patella IV yellow, tibia IV striped like femur, metatarsus IV red-brown (lighter distally), tarsus yellow-brown. Tibia I ventral spination: 3–3, long and strong.

External epigynum with two high circular openings (Fig. 191). Internal structure with globose spermathecae having narrow posterior necks (Fig. 190).

Diagnosis. Castianeira cincta differs from other *Castianeira* in its wide carapace (carapace index 71–75), cheliceral "rake"

in the female (Fig. 267), and the male genitalia (with a very short embolus).

Remarks. The presence of a thoracic groove and the eye arrangement clearly place this spider in the *Castianeira.*

Natural history. Nothing is known of the habits of this species.

Distribution. Panama (Map 12).

Records. CANAL ZONE. Barro Colorado Island, Chilibre, Farfan, Mt. Hope, Summit.

Castianeira dentata Chickering
Figures 197–200, 271–273. Map 12.

Castianeira dentata Chickering, 1937, Trans. Amer. Microscop. Soc. 56(1):3–4, figs. 8, 19, 55, ♀, from Barro Colorado Island, Panama Canal Zone; in the Museum of Comparative Zoology, examined.

Castianeira pusilla Chickering, 1937, Trans. Amer. Microscop. Soc. 56(1):7–8, figs. 3, 47, ♂, from Barro Colorado Island, Panama Canal Zone; in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

MALE

Measurements. Based on 10 males: carapace length 1.40–1.60 mm; carapace width 1.05–1.15 mm; carapace index 72–76; sternum length 0.70–0.75 mm; sternum width 0.65–0.70 mm; sternum index 87–92.

Femur IV length 1.10–1.25 mm; femur IV width 0.35–0.40 mm; leg thickness index 30–34; leg length index 79–81.

Abdomen length 1.85–2.05 mm; abdomen width 0.95–1.10 mm; abdomen index 53–58.

Embolus length 0.21–0.25 mm; bulb length 0.62–0.67 mm; male genital index 17–19.

Description. Carapace dark brown and hairless. Eyes moderate, raised—posteriors equal, anterior median eyes larger and anterior lateral eyes smaller (Fig. 271). Head narrow (cephalic width index 47–50) and smoothly truncated anteriorly. Thoracic groove moderately weak.

Abdomen a wide oval, wider posteriorly, and totally covered by a deep red-brown dorsal sclerite with short plumose hairs and heavily punctate with three horizontal bands of white hairs (Fig. 272). First pair of abdominal setae thin, second pair strong and stout.

Sternum orange-brown, with some fine hairs.

Chelicerae red-brown, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin tooth; a small denticle just median and distal to the distal promargin tooth. Four heavy, serrated setae at the promargin side of each chelicera apex (not as heavy as in the female).

Coxae I and IV light brown, coxa III tan, and coxa II creamy white. Trochanter IV notch moderately small.

Femora all dark reddish brown (lightening to light yellow at distal end). Rest of legs I and II yellow; rest of leg III with striped patella-tibia (yellow with brown sides) and yellow-brown metatarsus and tarsus; rest of leg IV red-brown, with a yellow-orange tarsus. Legs moderately hirsute. Tibia I ventral spination: 3–3, moderately small (the proximal spines much smaller).

Pedipalp with no tibial apophysis. Tarsus with globose genital bulb drawn out into a long neck with a straight, thin embolus, slightly curved near tip (Figs. 199, 200).

FEMALE

Measurements. Based on holotype and 9 females, holotype listed first, range of all follows: carapace length 1.65 mm, 1.60–1.75 mm; carapace width 1.25 mm, 1.15–1.30 mm; carapace index 75, 73–76; sternum length 0.85 mm, 0.75–0.90 mm; sternum width 0.75 mm, 0.70–0.80 mm; sternum index 89, 88–96.

Femur IV length 1.35 mm, 1.20–1.50 mm; femur IV width 0.40 mm, 0.35–0.45 mm; leg thickness index 30, 29–31; leg length index 81, 78–87.

Abdomen length 2.40 mm, 1.95–2.40 mm; abdomen width 1.65 mm, 1.40–1.80 mm;

abdomen index 69, 67–80; dorsal sclerite length 1.85 mm, 1.75–2.15 mm.

Description. Carapace fairly wide, dark orange-brown with some brown markings, and hairless. Eyes moderate, posteriors equal, anterior median eyes larger and anterior lateral eyes smaller. Eyes bordered in black. Head narrow (cephalic width index 51–57) and smoothly truncated anteriorly. Thoracic groove moderately weak.

Abdomen a wide oval, with a very large red-brown dorsal sclerite (three quarters length of abdomen), and covered with short, light hairs. Epigastric sclerite and small inframammilliary sclerite red-brown. Ventrum creamy white. First pair of abdominal setae very thin, second pair moderately strong and stout.

Sternum dark yellow-brown, wide, with some fine hairs but no setae.

Chelicerae orange-brown, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth; a small denticle just median and distal to the distal promargin tooth. Four heavy, serrated spines at the promargin side of each chelicera apex (Fig. 273).

Coxae all very light yellow, three anterior ones slightly lighter. Trochanter IV notch small.

Femora I–III striped with brown lateral sides on yellow—dark brown in femur III; femur IV dark red-brown. Rest of legs I and II light yellow-brown; rest of leg III striped like femur, except tarsus yellow-brown; rest of leg IV, patella-tibia striped with red-brown sides on yellow, metatarsus dark red-brown, tarsus yellow-brown. Legs moderately hirsute. Tibia I ventral spination: 3–3, moderately long and strong.

External epigynum with low, flared openings (Fig. 198). Internal structure of somewhat globose spermathecae with thick posterior necks (Fig. 197).

Diagnosis. A wide carapace (carapace index 72–76), small size, a heavy, fork-pronged cheliceral "rake" on the female, and distinctive male genitalia (Fig. 200) distinguish *Castianeira dentata* from all other *Castianeira*.

Remarks. The male and female of this species were originally described as two species, but except for the cheliceral "rake" in the female, the two (*C. dentata*, the female, and *C. pusilla*, the male) are quite within the range of normal sexual dimorphism.

Natural history. Nothing is known of the habits of this species.

Distribution. Panama (Map 12).

Records. PANAMA. Portobelo, El Valle. CANAL ZONE. Barro Colorado Island, Chilibre, Experimental Gardens, Forest Reserve, Fort Sherman, France Field, Gamboa, Madden Dam, Summit.

Castianeira trimac new species

Figures 201–204, 268–270. Map 12.

Holotype. Male from Forest Preserve, Panama Canal Zone, VII-1939 (A. M. Chickering); in the Museum of Comparative Zoology. The specific name is an arbitrary combination of letters.

MALE

Measurements. Based on one male holotype: carapace length 1.10 mm; carapace width 0.80 mm; carapace index 70; sternum length 0.60 mm; sternum width 0.50 mm; sternum index 81.

Femur IV length 0.90 mm; femur IV width 0.20 mm; leg thickness index 23; leg length index 80.

Abdomen length 1.25 mm; abdomen width 0.75 mm; abdomen index 62.

Embolus length 0.03 mm; bulb length 0.42 mm; male genital index 6.

Description. Very small spider. Carapace yellow-brown with darker brown markings radiating from the center of the thoracic region, shiny and hairless. Eyes moderate, with anterior median eyes larger. Eyes bordered in black. Carapace narrowed in cephalic region (cephalic width index 49)

and truncated anteriorly. No thoracic groove, but a distinct impression.

Abdomen oval, with a full dorsal sclerite and a pattern of white hair bands and spots (on light background)—a horizontal band over sclerite, a divided band just posterior to sclerite, and three spots in a horizontal line at posterior end—and a wide horizontal band of dark yellow just posterior to midline, rest brown (Fig. 269). Epigastric sclerite mottled brown. Ventrum with a full yellow sclerite and a small dark brown inframammilliary sclerite. Both pairs of abdominal setae extremely thin.

Sternum shield-shaped, shiny, hairless, and mottled brown—darker near each coxa.

Chelicerae light yellow-brown, with two moderately small retromargin teeth and three promargin teeth, a median one larger and a proximal one smaller than the retromargin teeth, and a very small one medial and distal to the larger promargin tooth.

Coxae cream-white (I and II with brown sides). Trochanter IV notch absent.

Femora I and II brown; femora III and IV striped dark brown sides and dorsum, rest yellow-white. Rest of leg I and II creamy white; rest of leg III striped, with patella-tibia and metatarsus yellow-white with dark brown sides, yellow-white tarsus; rest of leg IV, patella brown, tibia yellow-white with dark brown sides, metatarsus dark brown, tarsus creamy white. Legs moderately lightly hirsute. Tibia I ventral spination: 3–3, moderately long and strong.

Pedipalp with a short, blunt, tibial apophysis. Tarsus with a globose genital bulb drawn out into a long neck terminating with a short, crooked embolus (Figs. 201, 202).

FEMALE

Measurements. Based on 6 females: carapace length 1.20–1.30 mm; carapace width 0.80–0.85 mm; carapace index 66–69; sternum length 0.60–0.70 mm; sternum width 0.50–0.60 mm; sternum index 82–85.

Femur IV length 0.95–1.05 mm; femur IV width 0.20–0.25 mm; leg thickness index 22–25; leg length index 78–82.

Abdomen length 1.30–1.85 mm; abdomen width 0.80–1.10 mm; abdomen index 57–63; dorsal sclerite length 0.55–0.75 mm; dorsal sclerite width 0.50 mm; dorsal sclerite index 65–91.

Description. Very small spider. Carapace yellow-brown with darker brown markings radiating from the center of the thoracic region, shiny and hairless. Eyes moderate, with anterior median eyes larger. Eyes bordered in black. Carapace narrowed in cephalic region (cephalic width index 55–58) and truncated anteriorly. No thoracic groove, but a distinct impression.

Abdomen oval, with moderate orange-brown sclerite and a pattern of white hair bands and spots (on light background)—a horizontal band over sclerite, a divided band just posterior to sclerite, and three spots in a horizontal line at posterior end—and a wide horizontal band of dark yellow just posterior to midline, rest brown (Fig. 268). Epigastric sclerite mottled brown. Ventrum creamy white with brown-black spot just anterior to spinnerets. Both pairs of abdominal setae extremely thin.

Sternum shield-shaped, shiny, hairless, and mottled brown—darker near each coxa.

Chelicerae light yellow-brown, with two moderately small retromargin teeth and three promargin teeth, a median one larger and a proximal one smaller than the retromargin teeth, and a very small one medial and distal to the larger promargin tooth. Single large, serrated "claw" at promarginal cheliceral apex (Fig. 270).

Femora I and II brown; femora III and IV striped dark brown sides and dorsum, rest yellow-white. Rest of legs I and II creamy white; rest of leg III striped, with patella-tibia and metatarsus yellow-white with dark brown sides, yellow-white tarsus; rest of leg IV, patella brown, tibia yellow-white with dark brown sides, metatarsus dark brown, tarsus creamy white. Legs

moderately lightly hirsute. Tibia I ventral spination: 3–3, long and strong.

External epigynum with two small semicircular openings directed posteriorly (Fig. 204). Internal structure with two elongated spermathecae, wider in middle (Fig. 203).

Diagnosis. Castianeira trimac differs from other *Castianeira* in its abdominal pattern (three light spots in a horizontal row at the posterior end), a single heavy "claw" at the apex of each chelicera in the females (Fig. 270), and the embolus of the male (Fig. 202).

Remarks. This is the smallest of all known species of *Castianeira*.

Natural history. Nothing is known of the habits of this species.

Distribution. Panama (Map 12).

Records. CANAL ZONE. Barro Colorado Island, Forest Reserve, Summit.

Mazax O. P.-Cambridge

Mazax O. P.-Cambridge, 1898, Biol. Centrali-Americana Arachnida 1:275–276, pl. 34, fig. 2, ♀. Type-species by monotypy: *Mazax spinosa* O. P.-Cambridge, *op. cit.*, 1:276, pl. 34, fig. 2. ♀, from Teapa, Tabasco, Mexico; in the British Museum (Natural History), examined. The specific name is a junior homonym, the new name is *Mazax pax*.

Characteristics. Two rows of eyes, the posterior row wider than the anterior row; anterior row recurved, the posterior row straight or slightly procurved; eyes moderately large and approximately equal, with the anterior median eyes slightly smaller than the anterior lateral eyes.

Thoracic groove moderate to extremely weak. Cephalic region of carapace moderately narrow (cephalic width index 53–64).

Abdomen with a distinct, rugose, anterior petiole (Figs. 282–285). Constriction in male abdomen.

Tibia I ventral spination usually paired and moderately long: 3–3, 4–4, 5–5, or 6–6 (except *M. ajax* with 2–1, small spines).

Carapace length 1.60–2.85 mm, with a carapace index of 54–66 (moderate).

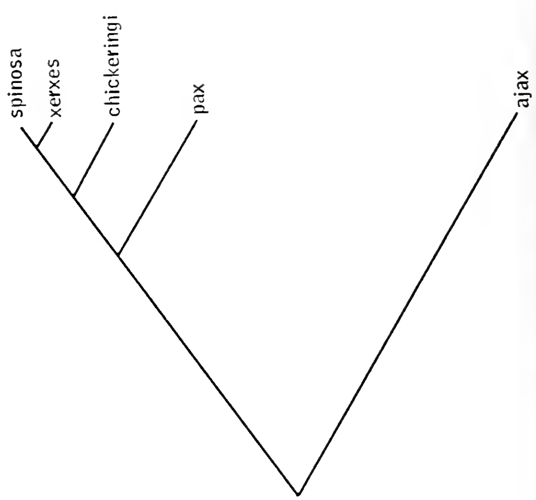


Diagram 2. A cladogram of *Mazax*.

Distribution. Mexico, West Indies, Central and South America (Map 13).

Discussion: This genus is compact and monophyletic, with the *spinosa* and *pax* groups closely related and the *ajax* group very different. Diagram 2 is a simple cladogram that shows the relationships of the species.

Key to the Males and Females of *Mazax*

1a. Tibia I ventral spination: 2–1 or 3–3 2

1b. Tibia I ventral spination: 4–4, 5–5, or 6–6 .. 3

2a. Tibia I ventral spination: 2–1; embolus long and straight (Fig. 238), spermathecae very long (Fig. 239) (southern Mexico) .... *ajax* p. 268

2b. Tibia I ventral spination: 3–3; embolus short and twisted (Fig. 236), spermathecae short (Fig. 233) (Mexico and Central America) .... *pax* p. 264

3a. Carapace bicolored (yellow-orange cephalic region, red-brown posterior thoracic region) (Fig. 280) (Costa Rica) .... *xerxes* p. 261

3b. Carapace not bicolored 4

4a. Male abdomen strongly impressed in middle (Fig. 283); tibia I ventral spination of females 5–5 or 6–6 (West Indies and Central America) .... *spinosa* p. 259

4b. Male abdomen weakly impressed (Fig. 282); tibia I ventral spination of females 4–4 (Jamaica) .... *chickeringi* p. 262

THE *SPINOSA* GROUP

Characteristics. Tibia I ventral spination 4–4 to 6–6 and carapace devoid of white hairs.

Discussion. Of the three species in this group, *Mazax spinosa* and *M. xerxes* are most clearly related. *M. chickeringi*, found only on Jamaica, is somewhat smaller and more different.

Mazax spinosa (Simon), new combination
Figures 230–232, 283, 284. Map 13.

Castianeira spinosa Simon, 1897, Proc. Zool. Soc. London: 882–883, ♂, ♀. One male and four female syntypes from St. Vincent, British West Indies; in the British Museum (Natural History), examined, and male lectotype designated here. This is not *Mazax spinosa* O. P.-Cambridge, 1898 (= *Mazax pax* n.n.).

Mazax plana F. P.-Cambridge, 1899, Biol. Centrali-Americana Arachnida 2:83, pl. 6, fig. 11, ♀, from Guatemala; in the British Museum (Natural History), examined. NEW SYNONYMY. Chickering, 1937, Trans. Amer. Microscop. Soc. 56:33, figs. 2, 27.

Mazax segregata Chamberlin, 1925, Bull. Mus. Comp. Zool. 67:221, ♀, from Barro Colorado Island, Panama Canal Zone; in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

MALE

Measurements. Based on lectotype and 10 males, lectotype, listed first, but not included in range of rest, which follows: carapace length 1.85 mm, 2.15–2.50 mm; carapace width 1.15 mm, 1.20–1.45 mm; carapace index 62, 57–59; sternum length 0.90 mm, 1.05–1.30 mm; sternum width 0.70 mm, 0.70–0.80 mm; sternum index 75, 60–70.

Femur IV length 1.60 mm, 2.05–2.45 mm; femur IV width 0.30 mm, 0.30–0.35 mm; leg thickness index 17, 14–17; leg length index 88, 90–97.

Abdomen length 2.50 mm, 2.75–3.70 mm; abdomen width 0.95 mm, 1.00–1.25 mm; abdomen index 38, 34–39; petiole length 0.40, 0.60–0.75 mm.

Embolus length 0.06 mm, 0.05–0.07 mm; bulb length 0.69 mm, 0.73–0.85 mm; male genital index 8, 6–8.

Description. Carapace red-brown, with a lightly granulose surface, and hairless. Eyes moderately large and approximately equal, the anterior medians slightly smaller than the rest. The anterior row recurved, the posterior straight. Carapace narrowed in head region (cephalic width index 53–58) and truncated smoothly anteriorly. Thoracic groove very small and faint.

Abdomen elongated, constricted in middle, with a fairly long, rugose, anterior petiole, and covered with a full, shiny, maroon-brown dorsal sclerite (Fig. 283). Sclerite slightly lighter at constriction, with some white plumose hairs. Whole dorsum covered with sparse, simple hairs. Epigastric sclerite (forming petiole anteriorly), full ventral sclerite, and a very small inframammilliary sclerite all red-brown. A pair of moderately large spines on tubercles at anterior end of dorsal sclerite (homologous to second pair of abdominal setae).

Sternum orange-brown, with some very long hairlike setae.

Chelicerae dark orange-brown, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth. A very small denticle just distal and slightly median to the larger promargin tooth.

Coxae II and III yellow, I brown and IV orange-brown. Trochanter IV notch very shallow but present.

All femora with dark red-brown sides, but the rest of femur I with a brown base and yellow-white distally, of femur II yellow-white, of femora III and IV dark yellow. Rest of legs I and II yellow-white, with middle two thirds of metatarsus I red-brown and metatarsus II yellow; rest of leg III yellow, with sides of patella-tibia and metatarsus light red-brown, tarsus yellow-white; rest of leg IV with yellow

patella with red-brown sides, red-brown tibia with a light yellow distal tip, red-brown metatarsus, and yellow-white tarsus. Legs lightly hirsute. Tibia I ventral spination: 4–4, moderate.

Pedipalp with a small, pointed, tibial apophysis. Tarsus with a globose genital bulb drawn out into a long neck with a small, twisted, sclerotized embolus (Fig. 230).

FEMALE

Measurements. Based on 11 females: carapace length 2.30–2.75 mm; carapace width 1.35–1.60 mm; carapace index 56–60; sternum length 1.15–1.40 mm; sternum width 0.80–0.90 mm; sternum index 65–72.

Femur IV length 2.15–2.55 mm; femur IV width 0.30–0.35 mm; leg thickness index 14–16; leg length index 91–99.

Abdomen length 2.60–3.85 mm; abdomen width 1.05–2.20 mm; abdomen index 40–60; dorsal sclerite length 0.95–1.45 mm; dorsal sclerite width 0.95–1.35 mm; dorsal sclerite index 76–105; petiole length 0.40–0.65 mm.

Description. Carapace red-brown, with a lightly granulose surface. Eyes large and approximately equal, anterior eyes recurved and posterior eyes straight when viewed dorsally. Carapace somewhat narrowed in head region (cephalic width index 57–63) and smoothly truncated anteriorly. Thoracic groove extremely small and faint.

Abdomen a long oval, with an anterior petiole and a dorsal sclerite. The petiole dark red-brown and heavily rugose; dorsal sclerite extends about two-fifths of the way back and is dark red-brown, shiny, and spineless. Abdomen almost hairless and shiny brown-grey with a thin, white, horizontal band just anterior to posterior edges of the dorsal sclerite, which covers the median portion of the band (Fig. 284). Ventral abdomen with a dark red-brown epigastric sclerite (which also forms the petiole), with two beaded stripes from sides of sclerite posteriorly. Sides of abdomen have a large longitudinal white spot on each side. First pair of abdominal setae absent, second pair very thin and long.

Sternum orange-brown, indented slightly at each coxa, and covered with hairlike setae.

Chelicerae orange-brown, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth. A very small denticle just distal and slightly median to the larger promargin tooth.

Coxae II and III yellow, I yellow-brown and IV light red-brown. Trochanter IV notch very shallow but present.

Femora all more or less striped, with sides brown (increasing towards IV) and light areas yellow in I and II, dark yellow in III, and yellow-brown in IV. Rest of I, II, and III light yellow; of IV yellow, with sides of tibia and metatarsus brown. Legs lightly hirsute. Tibia I ventral spination: 5–5, long and thin.

External epigynum with two, small, widely separated openings (Fig. 232). Internal structure with globose spermathecae drawn out into moderately thin posterior necks (Fig. 231).

Diagnosis. *Mazax spinosa* (Simon) differs from other *Mazax* in its monocolored carapace, the highly constricted abdomen of the male (Fig. 283), and the shiny dorsal abdominal sclerite of the female.

Remarks. The males of *M. spinosa* have a tibia I spination of 4–4, whereas the females have 5–5 and sometimes 6–6. The type is smaller than the populations measured in Panama and tends, with several other West Indian *M. spinosa*, to have a slightly rougher sculpture on the anterior half of the male abdomen.

The priority of Simon's name necessitates the change of *Mazax spinosa* O. P.-Cambridge to *Mazax pax* n.n.

Natural history. *Mazax spinosa* is found walking with a jerky gait over dead leaves

in tropical forest. The shiny abdominal sclerites and the large abdominal spines in the male suggest mimicry of certain dark myrmicine ants.

Distribution. West Indies, Central America, and Panama (Map 13).

Records. PANAMA. Boquete.

CANAL ZONE. Barro Colorado Island, Farfan, Forest Reserve, France Field, Gamboa, Gatun, Madden Dam, Pedro Miguel, Summit.

BRITISH WEST INDIES. *St. Lucia, St. Vincent.*

Mazax xerxes new species

Figures 226–229, 280, 281. Map 13.

Holotype. Male from Turrialba, Costa Rica, VII-23/VIII-13-1965 (A. M. Chickering); in the Museum of Comparative Zoology. The specific name is a noun in apposition based on the name of a Persian king.

MALE

Measurements. Based on one male holotype: carapace length 2.30 mm; carapace width 1.35 mm; carapace index 58; sternum length 1.20 mm; sternum width 0.75 mm; sternum index 65.

Femur IV length 2.00 mm; femur IV width 0.30 mm; leg thickness index 15; leg length index 86.

Abdomen length 3.55 mm; abdomen width 1.10 mm; abdomen index 31; petiole length 0.65 mm.

Embolus length 0.07 mm; bulb length 0.85 mm; male genital index 8.

Description. Carapace with light yellow-orange cephalic and anterior thoracic regions, and dark red-brown posterior thoracic region (Fig. 280). Surface very finely granulose and hairless. Eyes large and approximately equal (anterior median eyes slightly smaller than laterals); anterior eyes recurved and the posterior eyes straight when viewed dorsally (Fig. 281). Ocular region dark red-brown. Carapace narrowed in head region (cephalic width index 59) and truncated smoothly anteriorly. Thoracic groove extremely weak.

Abdomen elongated, constricted in middle, with a fairly long, rugose petiole, and covered with a full, shiny, maroon dorsal sclerite. Sclerite slightly lighter at constriction, with some white plumose hairs. Whole dorsum covered with sparse simple hairs. Epigastric sclerite (forming petiole anteriorly), full ventral sclerite, and a moderate inframammilliary sclerite all dark red-brown. No spines or abdominal setae on the dorsal sclerite.

Sternum yellow, with some very long, hairlike setae.

Chelicerae orange-brown and reticulated brown, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth. A very small denticle just distal and slightly medial to the larger promargin tooth.

Coxae II and III light yellow, I yellow and IV yellowish brown. Trochanter IV notch very shallow but present.

Femur I, basal half dark red-brown, light yellow distally with brown sides; femora II, III, and IV yellow with some red-brown on the sides (only on sides of distal end of femur IV). Rest of legs I and II yellow-white (distal halves of metatarsi slightly darker); rest of leg III yellow, with red-brown sides on patella-tibia, a slightly darker metatarsus, and a creamy white tarsus; rest of leg IV with yellow patella (with a trace of red-brown on sides), dark red-brown tibia with yellow tips, metatarsus yellow with wide bands of red-brown on the sides, and light yellow tarsus. Legs lightly hirsute. Tibia I ventral spination: 5–5, long and thin, the proximal pair distinctly smaller.

Pedipalp with a small, pointed, tibial apophysis. Tarsus with a globose genital bulb drawn out into a long neck with a small, twisted, sclerotized embolus (Figs. 228, 229).

FEMALE

Measurements. Based on one female: carapace length 2.50 mm; carapace width 1.50 mm; carapace index 59; sternum length 1.30 mm; sternum width 0.85 mm; sternum index 66.

Femur IV length 2.40 mm; femur IV width 0.35 mm; leg thickness index 15; leg length index 96.

Abdomen length 4.25 mm; abdomen width 1.85 mm; abdomen index 44; dorsal sclerite length 1.20 mm; dorsal sclerite width 1.05 mm; dorsal sclerite index 89; petiole length 0.55 mm.

Description. Carapace with light yellow-orange cephalic and anterior thoracic regions, and dark maroon-brown posterior thoracic region. Surface very finely granulose and hairless. Eyes large and approximately equal, anterior eyes recurved and the posterior eyes straight when viewed dorsally. Ocular region dark red-brown. Carapace narrowed in head region (cephalic width index 61) and truncated smoothly anteriorly. Thoracic groove extremely weak.

Abdomen oval, with an anterior maroon-brown rugose petiole and a moderately small, shiny, dark red-brown dorsal sclerite. Rest of dorsal abdomen brown-purple, with sparse light, simple hairs and a slightly lighter horizontal band at posterior edge of sclerite. Ventrum with a dark red-brown epigastric sclerite (which continues anteriorly and dorsally as the petiole), a very small red-brown inframammilliary sclerite, and a pair of beaded light stripes from the sides of the epigastric furrow posteriorly. First pair of abdominal setae absent, second pair very thin and long.

Sternum orange-brown, indented slightly at each coxa, and covered with hairlike setae.

Chelicerae orange-brown and reticulated brown, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth. A very small denticle just distal and slightly median to the larger promargin tooth.

Coxae II and III light yellow, I yellow-orange, IV yellow-brown. Trochanter IV notch very shallow but present.

Femur I, basal half dark red-brown, light yellow distally with brown sides; femora II, III, and IV yellow with some red-brown on the sides (only on sides of distal end of femur IV). Rest of legs I and II yellow-white (distal halves of metatarsi slightly darker); rest of leg III yellow, with red-brown sides on patella-tibia, a slightly darker metatarsus, and a creamy white tarsus; rest of leg IV with yellow patella, yellow tibia with dark red-brown sides near proximal end, and a creamy white tarsus. Legs lightly hirsute. Tibia I ventral spination: 5–5, very long and thin.

External epigynum with two small, widely separated openings (Fig. 227). Internal structure with globose spermathecae and narrow posterior necks (Fig. 226).

Diagnosis. *Mazax xerxes* differs from all other *Mazax* in its bicolored carapace (cephalic and anterior thoracic regions yellow).

In addition to the difference in color, the male of *M. xerxes* has no dorsal abdominal spines and has a tibia I ventral spination of 5–5.

Natural history. Nothing is known of the habits of this species, though it is probably an ant mimic, and the model ant or ants probably have yellowish heads.

Distribution. Costa Rica (Map 13).

Records. COSTA RICA. Turrialba.

Mazax chickeringi new species
Figures 222–225, 282. Map 13.

Holotype. Male from Trafalger Rd., St. Andrew, Jamaica, 19/21-XI-1963 (A. M. Chickering); in the Museum of Comparative Zoology. The species is named after Dr. A. M. Chickering.

MALE

Measurements. Based on holotype and 9 males, holotype listed first, range of all follows: carapace length 2.00 mm, 1.70–2.10 mm; carapace width 1.25 mm, 1.10–1.30 mm; carapace index 63, 63–66; sternum length 1.00 mm, 0.85–1.05 mm; sternum width 0.75 mm, 0.70–0.75 mm; sternum index 77, 72–79.

Femur IV length 1.70 mm, 1.50–1.80 mm; femur IV width 0.30 mm, 0.25–0.30 mm; leg thickness index 17, 17–18; leg length index 86, 84–89.

Abdomen length 2.55 mm, 2.20–2.65 mm; abdomen width 1.05 mm, 0.95–1.15 mm; abdomen index 42, 41–45; petiole length 0.40 mm, 0.30–0.40 mm.

Embolus length 0.06 mm, 0.05–0.06 mm; bulb length 0.70 mm, 0.61–0.70 mm; male genital index 8, 7–8.

Description. Carapace deep red-brown with a finely granulose surface (heavier on thoracic region) and hairless. Eyes large and equal, except anterior median eyes somewhat smaller than the rest. Anterior row slightly recurved, posterior row straight. Carapace narrower in head region (cephalic width index 54–58) and smoothly truncated anteriorly. Thoracic groove present as a slightly elongated notch.

Abdomen dark red-brown, elongated, with an anterior rugose petiole and a full dorsal sclerite with a moderate constriction, but smooth and shiny posterior to it, with some white hairs. Epigastric sclerite, a full ventral sclerite, and a minute inframammilliary sclerite red-brown. A pair of heavy dorsal spines on tubercles at anterior of abdomen (just posterior to petiole).

Sternum orange-brown, with a few hair-like, long setae. Pedicel short.

Chelicerae dark red-brown with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth. A very small, but clear, denticle just distal and slightly median to the larger promargin tooth.

Coxae all deep yellow (posterior pair darker). Trochanter IV notch absent.

Femora all deep yellow with red-brown sides. Rest of legs I and II yellow; rest of legs III and IV dark yellow; all tarsi somewhat lighter. Legs lightly hirsute. Tibia I ventral spination: 4–4, moderately small and weak.

Pedipalp with no tibial apophysis. Tarsus with a globose bulb drawn out into a neck with a small twisted embolus at its tip. Medial palpal duct loop small (Figs. 224, 225).

FEMALE

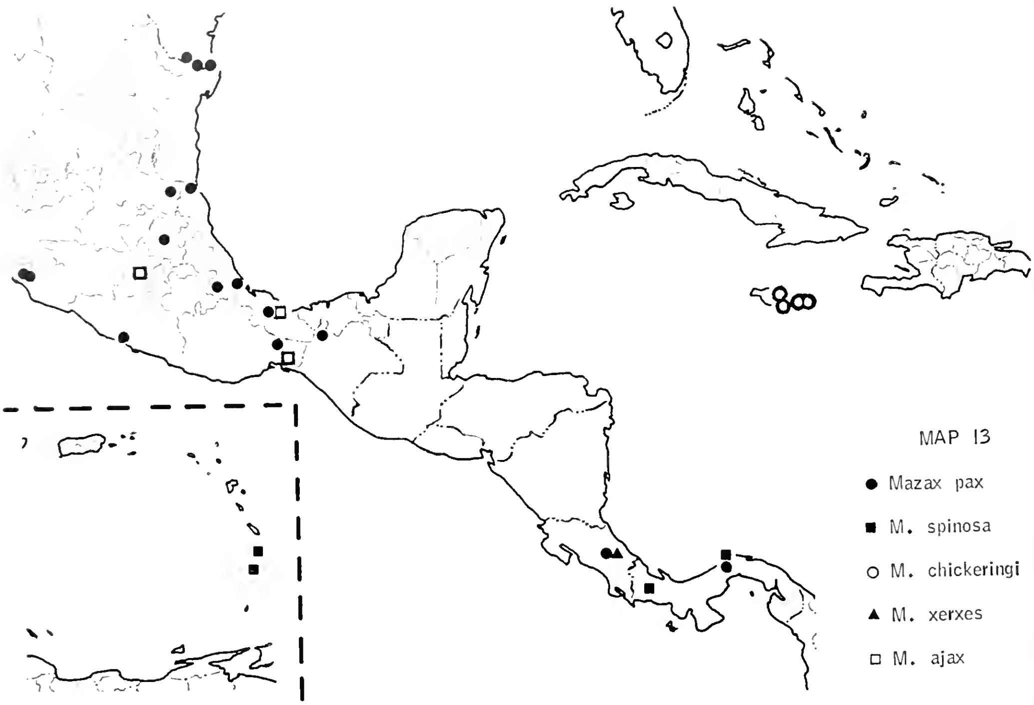
Measurements. Based on 10 females: carapace length 1.90–2.30 mm; carapace width 1.20–1.50 mm; carapace index 62–65; sternum length 0.95–1.15 mm; sternum width 0.75–0.85 mm; sternum index 74–79.

Femur IV length 1.65–1.95 mm; femur IV width 0.30–0.35 mm; leg thickness index 17–19; leg length index 83–90.

Abdomen length 2.55–3.30 mm; abdomen width 1.30–2.30 mm; abdomen index 49–66; dorsal sclerite length 0.85–1.10 mm; dorsal sclerite width 0.90–1.10 mm; dorsal sclerite index 97–114; petiole length 0.25–0.30 mm.

Description. Carapace deep red-brown with a finely granulose surface (heavier on thoracic region) and hairless. Eyes large and equal, except anterior median eyes somewhat smaller than the rest. Anterior row slightly recurved, posterior row straight. Carapace narrower in head region (cephalic width index 57–61) and smoothly truncated anteriorly. Thoracic groove present as a slightly elongated notch.

Abdomen oval, with an anterior rugose petiole and a moderate, finely granulose, dorsal sclerite, both red-brown. Epigastric sclerite red-brown. Rest of dorsum and ventrum purplish brown, the ventrum with some light, beaded lines running from epigastric furrow to a small red-brown in-



framammilliary sclerite. Abdominal setae not discernible. No abdominal dorsal spines.

Sternum red-brown with a few hairlike, long setae. Pedicel short.

Chelicerae dark red-brown, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth. A very small, but clear, denticle just distal and slightly median to the larger promargin tooth.

Coxae I–III deep yellow, IV yellow-orange. Trochanter IV notch absent.

Femur I red-brown; femora II–IV striped dark yellow with red-brown sides. Rest of legs I and II yellow; rest of III and IV orange, with darker patellae; all tarsi yellow-white. Legs lightly hirsute. Tibia I ventral spination: 4–4, moderately long and thin.

External epigynum with two small, flared openings (Fig. 223). Internal structure of spermathecae with globose anterior bulb and moderately narrow necks (Fig. 222).

Diagnosis. Males of *Mazax chickeringi* have a much shallower abdominal impression than do the other *Mazax* species, and the females have a tibia I ventral spination of 4–4 (females of *M. spinosa* have 5–5 or 6–6). In addition, the horizontal light stripe on the abdomens of *M. spinosa* and *M. xerxes* is absent.

Distribution. Jamaica (Map 13).

Records. JAMAICA. *St. Ann Parish, Clarendon Parish, Kingston Parish, St. Andrew Parish, St. Catherine Parish, St. Thomas Parish.*

The *pax* Group

Mazax pax new name

Figures 233–236, 285. Map 13.

Mazax spinosa O. P.-Cambridge, 1898, Biol. Centrali-Americana Arachnida 1:276, pl. 34, fig. 2, ♀, from Teapa, Tabasco, Mexico; in the British Museum (Natural History), examined. (Not *Mazax spinosa* (Simon) 1897.)

Mazax spinosa: Chickering, 1937, Trans. Amer. Microscop. Soc. 56(1):33–34, figs. 10, 24, 68, ♂, ♀.

Name. The new specific name is a Latin noun in apposition meaning "peace."

MALE (Mexican)

Measurements. Based on 8 males: carapace length 1.60–1.90 mm; carapace width 0.95–1.15 mm; carapace index 59–63; sternum length 0.75–0.90 mm; sternum width 0.60–0.65 mm; sternum index 71–80.

Femur IV length 1.20–1.60 mm; femur IV width 0.25–0.30 mm; leg thickness index 18–22; leg length index 72–85.

Abdomen length 2.00–2.60 mm; abdomen width 0.85–1.05 mm; abdomen index 36–46; petiole length 0.30–0.40 mm.

Embolus length 0.05–0.07 mm; bulb length 0.56–0.68 mm; male genital index 7–11.

Description. Carapace yellow-brown, with lightly granulose surface and a few white plumose hairs. Some long setae in cephalic region. Eyes moderately large, approximately equal, the anterior eyes recurved and the posterior eyes straight when viewed dorsally. Carapace narrower in head region (cephalic width index 53–61) and smoothly truncated anteriorly. Thoracic groove absent (only slight indentation remaining).

Abdomen drop-like (widening posteriorly), with an anterior red-brown rugose petiole and a full dorsal sclerite. Dorsal sclerite with a strong constriction in the middle, very rough and dark orange anterior to constriction, but smooth and shiny posterior to it, with four wide, horizontal, red-brown bands on an orange background. Sparse, simple hair over the whole dorsum. A pair of strong spines on tubercles at anterior end of dorsal sclerite. Epigastric sclerite (which also forms the petiole) red-brown. A full, yellow-orange, ventral sclerite.

Sternum yellow, with sparse, hairlike setae. Short pedicel.

Chelicerae light yellow-brown, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth. A very small but clear denticle just distal and slightly median to the larger promargin tooth.

Coxae I–III yellow-white, coxa IV light yellow-brown. Trochanter IV notch almost absent (just a very slight dip).

Femora I and II light yellow; femora III and IV yellow-brown. Rest of legs I and II light yellow, with light red-brown metatarsus I and creamy white tarsi; rest of legs III and IV brownish yellow, with slightly darker tibia IV with light distal ends, red-brown metatarsus IV, and light, creamy white tarsi. Legs moderately hirsute. Tibia I ventral spination: 3–3, thin and weak.

Pedipalp with a small, pointed, tibial apophysis. Tarsus with a globose genital bulb drawn out into a long neck with a small, thin, twisted embolus (Figs. 235, 236).

FEMALE (Mexican)

Measurements. Based on holotype and 8 females, holotype listed first, range of all follows: carapace length 1.80 mm, 1.80–2.20 mm; carapace width 1.10 mm, 1.10–1.30 mm; carapace index 61, 58–63; sternum length 0.90 mm, 0.90–1.10 mm; sternum width 0.65 mm, 0.65–0.75 mm; sternum index 72, 67–78.

Femur IV length 1.40 mm, 1.30–1.75 mm; femur IV width 0.30 mm, 0.30–0.40 mm; leg thickness index 21, 19–23; leg length index 77, 72–83.

Abdomen length 2.40 mm, 1.75–2.80 mm; abdomen width 1.35 mm, 1.15–1.70 mm; abdomen index 56, 54–65; dorsal sclerite length 1.40 mm, 1.00–1.65 mm; dorsal sclerite width 1.05 mm, 0.95–1.45 mm; dorsal sclerite index 77, 77–129; petiole length 0.30, 0.30–0.45 mm.

Description. Carapace light red-brown, with lightly granulose surface and very

sparse, white plumose hairs. Some long setae in cephalic region. Eyes large and approximately equal, the anterior eyes recurved and the posterior eyes straight when viewed dorsally. Carapace narrower in head region (cephalic width index 55–63) and smoothly truncated anteriorly. Thoracic groove absent (only slight indentation remaining).

Abdomen oval, with an anterior petiole and dorsal sclerite. Petiole red-brown rugose; dorsal sclerite extends about halfway back, is red-brown and shiny, with a pair of spines on tubercles at the anterior end (Fig. 285). Whole abdomen covered with moderately long, thin hairs; greyish brown, with a thin light horizontal dorsal band about one third of the way from spinnerets. Ventral abdomen with a dark red-brown epigastric sclerite (which also forms the petiole) and two faint, beaded stripes running from the outside edges of the sclerite posteriorly.

Sternum orange, with sparse, hairlike setae. Pedicel moderately short.

Chelicerae light brown, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth. A very small but clear denticle just distal and slightly median to the larger promargin tooth.

Coxae I, II, and III yellow, coxa IV yellow-brown. Trochanter IV notch almost absent (just a very slight dip).

Femora I and II light brown at base and yellow-white at distal end, slightly darker on the sides; femur III brown on sides and yellow on edges; femur IV light brown. Rest of I and II yellow-white; rest of III yellow; rest of IV yellow, with light brown sections in center of tibia and proximal two thirds of metatarsus. Tibia I ventral spination: 3–3, moderately long.

External epigynum with two small, widely separated openings (Fig. 234). Internal structure with globose spermathecae drawn out into moderately thin posterior necks (Fig. 233).

MALE (Costa Rican)

Measurements. Based on 10 males: carapace length 1.65–1.90 mm; carapace width 1.00–1.10 mm; carapace index 58–61; sternum length 0.80–0.95 mm; sternum width 0.60–0.70 mm; sternum index 71–76.

Femur IV length 1.35–1.60 mm; femur IV width 0.25–0.30 mm; leg thickness index 17–19; leg length index 78–84.

Abdomen length 2.05–2.60 mm; abdomen width 0.90–1.05 mm; abdomen index 39–43; petiole length 0.55–0.65 mm.

Embolus length 0.04–0.05 mm; bulb length 0.62–0.68 mm; male genital index 6–8.

FEMALE (Costa Rican)

Measurements. Based on 10 females: carapace length 1.90–2.20 mm; carapace width 1.10–1.30 mm; carapace index 58–62; sternum length 0.95–1.05 mm; sternum width 0.70–0.75 mm; sternum index 69–74.

Femur IV length 1.55–1.80 mm; femur IV width 0.30–0.35 mm; leg thickness index 17–19; leg length index 79–85.

Abdomen length 2.15–2.60 mm; abdomen width 1.15–1.40 mm; abdomen index 53–58; dorsal sclerite length 1.00–1.10 mm; dorsal sclerite width 1.00–1.15 mm; dorsal sclerite index 94–103; petiole length 0.40–0.50 mm.

MALE (Panamanian)

Measurements. Based on 5 males: carapace length 2.05–2.35 mm; carapace width 1.20–1.35 mm; carapace index 55–58; sternum length 1.05–1.20 mm; sternum width 0.65–0.75 mm; sternum index 62–68.

Femur IV length 1.65–1.95 mm; femur IV width 0.35–0.40 mm; leg thickness index 19–21; leg length index 81–84.

Abdomen length 2.50–2.95 mm; abdomen width 1.05–1.20 mm; abdomen index 39–46; petiole length 0.40–0.55 mm.

TABLE 2. GEOGRAPHIC FORMS OF *MAZAX PAX*.

		Localities			
		PANAMA	COSTA RICA	MEXICO-TEXAS	COLIMA
Carapace Length (in mm)	♂	2.05–2.35	1.65–1.90	1.60–1.90	—
	♀	2.30–2.75	1.90–2.20	1.80–2.20	1.90–2.20
Leg Thickness Index	♂	19–20	17–19	19–22	—
	♀	17–20	17–19	19–23	21
White plumose hairs on carapace		Numerous	Numerous	Very sparse	Very sparse
Dorsal abdominal sclerite ends	♀	At impression	At impression	At impression	Posterior to impression
Color	♂	Orange to brown	Brown-black	Red-brown	—
	♀	Orange to red-brown	Red-brown to brown-black	Red-brown	Red-brown

Embolus length 0.06 mm; bulb length 0.63–0.70 mm; male genital index 8–9.

FEMALE (Panamanian)

Measurements. Based on 5 females: carapace length 2.30–2.75 mm; carapace width 1.35–1.50 mm; carapace index 55–59; sternum length 1.15–1.30 mm; sternum width 0.75–0.85 mm; sternum index 61–67.

Femur IV length 1.95–2.25 mm; femur IV width 0.35–0.40 mm; leg thickness index 17–20; leg length index 82–85.

Abdomen length 2.95–3.20 mm; abdomen width 1.45–1.65 mm; abdomen index 46–54; dorsal sclerite length 1.20–1.50 mm; dorsal sclerite width 1.20–1.45 mm; dorsal sclerite index 96–104; petiole length 0.40–0.70 mm.

Diagnosis. Mazax pax differs from all other *Mazax* species in its tibia I ventral spination of 3–3 and the presence of some white plumose hairs on the carapace.

Remarks. The type is from Mexico, and therefore the measurements and descriptions of the Mexican form are presented first, followed by measurements of the Costa Rican and Panamanian forms. Table 2 lists the differences in these three forms plus an additional Mexican form from Colima. Some of the discontinuities may be the result of discontinuous collecting; further collections from Mexico and Central America may clarify the situation.

This species exhibits moderately strong sexual dimorphism.

Natural history. Mazax pax is found on dead leaves in shady areas; it walks with an antlike gait, the first pair of legs raised to give the illusion of antennae. Both sexes appear to mimic small myrmicines.

Courtship, but not mating, of *M. pax* was observed. The male first perceives the presence of the female, often after momentarily touching her but sometimes apparently by vision. He then orients his axis at right angles to hers and stands less than an inch away. He vibrates his abdomen horizontally with three to five single jerks followed by a longer vibration. This cycle is repeated several times and then is followed by the vibration of the whole body, the spider moving rapidly up and down with all legs on the ground. This is often followed by jerky, short, forward hops while the male vibrates his pedipalps, raising the first pair of legs and the abdomen at each hop. The courtship observed was never continued beyond this

point; the female was apparently unreceptive.

M. pax spins a round, disclike, yellow-white egg case (in the same manner as *Castianeira longipalpus*—see *Natural history* under that species). Of twenty-eight egg cases studied, six had three eggs, thirteen had four eggs, seven had five eggs, and two had six eggs (an average of 4.2 eggs per case). Development time between egg laying and emergence of the spiderling from the egg case was approximately 30 days, the spiders spending their first instar in the case, emerging as second instars.

Distribution. Southernmost Texas south to Panama (Map 13).

Records. Texas. Cameron Co., Hidalgo Co., Starr Co.

MEXICO. *Colima, Guerrero, Hidalgo, Oaxaca, San Luis Potosi, Tabasco, Veracruz.*

COSTA RICA. Turrialba.

CANAL ZONE. Barro Colorado Island, Corozal, Fort Sherman, Gatun, Summit.

The *ajax* Group

Mazax ajax new species

Figures 237–240. Map 13.

Holotype. Male from 4 mi. NE of Acayucan, Mexico, 27-IV-1963 (W. J. Gertsch and W. Ivie); in the American Museum of Natural History. The specific name is a noun in apposition after the Greek warrior Ajax.

MALE

Measurements. Based on holotype and one male, holotype listed first, range of both follows: carapace length 2.95 mm, 2.65–2.95 mm; carapace width 1.60 mm, 1.50–1.60 mm; carapace index 54, 54–57; sternum length 1.35 mm, 1.35 mm; sternum width 0.85 mm, 0.85 mm; sternum index 64, 64.

Femur IV length 2.40 mm, 2.20–2.40 mm; femur IV width 0.40 mm, 0.35–0.40 mm; leg thickness index 16, 16; leg length index 82, 82–83.

Abdomen length 3.55 mm, 3.45–3.55 mm; abdomen width 1.25 mm, 1.25–1.30 mm; abdomen index 35, 35–37.

Embolus length 0.21 mm, 0.21–0.23 mm; bulb length 1.06 mm, 1.06–1.08 mm; male genital index 20, 20–21.

Description. Carapace very reddish dark red-brown, with a lightly granulose surface, and hairless. Eyes moderate and approximately equal, the anterior medians slightly smaller than the rest. The anterior row moderately recurved, and the posterior row slightly recurved. Carapace narrowed in head region (cephalic width index 59–61) and truncated smoothly anteriorly. Carapace reaching high apex longitudinally along median and falling off rapidly on both sides. Thoracic groove moderate.

Abdomen elongated (like *M. plana*), constricted in middle with a moderate rugose anterior petiole and covered with a full, dark red-brown dorsal sclerite lightly striated anterior to constriction and shiny behind it. Sclerite slightly lighter at constriction with some white plumose hairs. Whole dorsum covered with sparse, simple hairs. Epigastric sclerite (forming petiole anteriorly), almost full ventral sclerite, and small inframammilliary sclerite all red-brown. No spines or abdominal setae present.

Sternum orange-brown with some very long, hairlike setae.

Chelicerae orange-brown, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth. A very small denticle just distal and slightly median to the larger promargin tooth.

Coxae II and III dark yellow-brown, I and IV red-brown. Trochanter IV notch small.

Femur I light yellow with dark red-brown basal half extending as two stripes to distal end; femora II and III dark yellow, with red-brown sides; femur IV orange, with red-brown sides. Rest of legs I and II yellow—retrolateral sides of

patellae-tibiae lightly red-brown, metatarsus I light red-brown, tarsi lighter; rest of leg III dark yellow—both sides of patella-tibia red-brown and tarsus light yellow; rest of leg IV—patella-tibia yellow-orange, with red-brown sides, metatarsus red-brown, tarsus light yellow. Legs lightly hirsute. Tibia I ventral spination: 2–1, very small and weak at distal end.

Pedipalp with a very small, blunt, tibial apophysis. Tarsus with a globose genital bulb drawn out into a long neck with a fairly long, strong, straight, and sclerotized embolus (Figs. 237, 238).

FEMALE

Measurements. Based on one female: carapace length 2.85 mm; carapace width 1.60 mm; carapace index 56; sternum length 1.30 mm; sternum width 0.85 mm; sternum index 68.

Femur IV length 2.20 mm; femur IV width 0.40 mm; leg thickness index 18; leg length index 77.

Abdomen length 2.75 mm; abdomen width 1.30 mm; abdomen index 48; dorsal sclerite length 0.95 mm; dorsal sclerite width 0.90 mm; dorsal sclerite index 93.

Description. This specimen is light and probably not yet full pigmented. Carapace yellow-brown, with a lightly granulose surface, and hairless. Eyes moderate and approximately equal, the anterior medians slightly smaller than the rest. Eyes bordered in black. The anterior row moderately recurved, and the posterior row slightly recurved. Carapace narrowed in head region (cephalic width index 64) and smoothly truncated anteriorly. Carapace reaching high apex longitudinally along median and falling off rapidly on both sides. Thoracic groove moderate.

Abdomen oval, with a median constriction, a moderate orange-brown, lightly granulose, dorsal sclerite anterior to the constriction, and a yellow-brown anterior petiole. Rest of dorsum and ventrum brownish purple (lighter ventrally). Epigastric sclerite light yellow-brown and a very small, light red-brown, inframammilliary sclerite. No spines or abdominal setae present.

Sternum pale orange-white with some very long hairlike setae.

Chelicerae pale brown, with two moderate retromargin teeth and two promargin teeth, the distal one larger and the proximal one smaller than the retromargin teeth. A very small denticle just distal and slightly median to the larger promargin tooth.

Coxae II–IV creamy white, I light purplish brown. Trochanter IV notch small.

Femur yellow-white, with a dark brown basal half and two side stripes to distal end; femora II–IV yellow-white, with brown sides (especially dark on prolateral sides of femur II). Rest of legs I–III pale yellow-white, with retrolateral side of patella-tibia III and all of metatarsus I brownish; rest of leg IV pale yellow-white, with sides of patella-tibia brownish (darker on retrolateral side) and metatarsus IV brownish. Legs lightly hirsute. Tibia I ventral spination: 2–1, very small and weak at distal end.

Epigynum very distinct, with two large, slitlike vertical openings externally (Fig. 240) and a spermatheca with an anterior bulb and a long posterior neck ending in a smaller bulb internally (Fig. 239).

Diagnosis. Mazax ajax differs from all other *Mazax* species in its tibia I ventral spination (2–1 and very small) and its very different genitalia (Figs. 237–240).

Remarks. While this species undoubtedly belongs to *Mazax*, it is radically different from the other four species; the divergence in genitalic characters suggests an early separation from the rest of the genus.

Natural history. Nothing is known of the habits of this species, though it is probably an ant mimic.

Distribution. Southern Mexico (Map 13).

Records. MEXICO. *Mexico, Oaxaca, Veracruz.*

Myrmecotypus O. P.-Cambridge

Myrmecotypus O. P.-Cambridge, 1894, Biol. Centrali-Americana Arachnida 1:123–124, pl. 18, fig. 6, ♀. Type-species by monotypy: *Myrmecotypus fuliginosus* O. P.-Cambridge, *op. cit.*, 1:124, pl. 18, fig. 6, ♀, from Teapa, Tabasco, Mexico; in the British Museum (Natural History), examined.

Characteristics. Two rows of eyes, the posterior row much wider than the anterior row; both rows moderately recurved, the anterior more strongly than the posterior (except anterior row in *M. lineatus* almost straight); posterior eyes and anterior lateral eyes fairly small and equal, with anterior median eyes about twice the diameter of the anterior lateral eyes.

Thoracic groove never present but often a slight thoracic depression in its place. Cephalic region of carapace wide (cephalic width index 64–89 with *M. pilosus* accounting for values below 72).

Tibia I ventral spination 2–2, 3–3, or 4–4. Trochanter IV notch usually absent, with only an extremely small one if present.

Carapace length 1.75–5.75 mm, with a carapace index of 39–53 (fairly narrow).

Distribution. Mexico, Central and South America.

Discussion. The genitalic differences between the species groups of *Myrmecotypus* are very great, which suggests a monophyletic origin with convergent mimetic characteristics uniting the group.

M. niger is probably somewhat related to the *olympus* group. *M. pilosus* and *M. lineatus* are atypical, the former perhaps related to some Old World forms and the latter mysteriously unique.

Key to the Males and Females of *Myrmecotypus*

1a. Tibia I ventral spination: 2–2; eyes small; abdomen strongly constricted (Fig. 155) (eastern U. S.) .... *lineatus* p. 272
1b. Not as above, tibia I ventral spination: 3–3 or 4–4 2
2a. Coxae I and II bright white to yellow-white, much lighter than coxae III and IV 3
2b. Not as above, either coxae II and III or just coxa II light 6
3a. Carapace with a deep groove between the cephalic and thoracic regions; small (carapace length 1.75–2.30) 4
3b. No deep groove on carapace 5
4a. Dark brown-black carapace; distinct male and female genitalia (Figs. 253–257) (Panama) .... *orpheus* p. 277
4b. Orange-brown carapace; distinct male and female genitalia (Figs. 258–261) (Panama) .... *olympus* p. 275
5a. Large (carapace length 5.15–5.75 mm) with a longitudinal row of erect, dense hairs on thoracic region; distinct genitalia (Figs. 262–265) (Panama) .... *rettenmeyeri* p. 278
5b. Smaller (carapace length 2.45–2.65 mm) with distinct genitalia (Figs. 241–244) (Panama) .... *niger* p. 274
6a. Coxa II light yellow-white, rest of the coxae dark; long simple hairs on abdomen; distinct genitalia (Figs. 245–248) .... *pilosus* p. 280
6b. Coxae II and III much lighter than coxae I and IV 7
7a. External epigynum as in Fig. 251 (Mexico) .... *fuliginosus* p. 270
7b. External epigynum as in Fig. 250 (Panama) .... *lineatipes* p. 271

The *fuliginosus* Group

Characteristics. Coxae II and III yellow-white to white, other coxae darker. External epigynal openings moderate to small and medially directed. Tibia I ventral spination 3–3.

Discussion. The two species in this group, *Myrmecotypus fuliginosus* and *M. lineatipes*, are only known from a single female in each case and are closely related.

Myrmecotypus fuliginosus O. P.-Cambridge
Figures 251, 252. Map 14.

Myrmecotypus fuliginosus O. P.-Cambridge, 1894, Biol. Centrali-Americana Arachnida 1:124, pl. 18, fig. 6, ♀, from Teapa, Tabasco, Mexico; in the British Museum (Natural History), examined.

FEMALE

Measurements. Based on one female holotype: carapace length 2.35 mm; carapace width 1.20 mm; carapace index 52; sternum length 1.05 mm; sternum width 0.65 mm; sternum index 61.

Femur IV length 1.60 mm; femur IV width 0.35 mm; leg thickness index 21; leg length index 67.

Abdomen length 2.50 mm; abdomen width 1.95 mm; abdomen index 79; dorsal sclerite length 0.80 mm; dorsal sclerite width 0.80 mm; dorsal sclerite index 100.

Description. Carapace red-brown with some white hairs. Eyes small and equal, except the anterior median eyes almost twice the diameter of anterior laterals; both rows recurved when viewed dorsally, the posterior row almost two-fifths wider than the anterior row. Carapace somewhat narrowed in head region (cephalic width index 72) and squarely truncated anteriorly. Thoracic groove absent.

Abdomen wide, with a fairly small, red-brown dorsal sclerite, and covered with some white plumose hairs. Epigastric sclerite red-brown. Ventrum orange-brown. Small inframammilliary sclerite orange-brown. First pair of abdominal setae thin and long, second pair moderate and long.

Sternum red-brown, elongate, shield-shaped, slightly pinched at coxa III, and with some light hairs.

Chelicerae red-brown, with two moderate retromargin teeth, the distal a bit smaller than the proximal, and two promargin teeth, the distal one much larger and the proximal slightly smaller than the retromargin teeth.

Coxae I and IV dark orange-brown; II and III pale yellow-white. Trochanter IV notch very small.

Femur I with brown basal half and light yellow distal half, with a dorsal brown stripe; femur II yellow, with brown sides and short dorsal stripe at distal end; femora III and IV dark orange-brown. Rest of legs I and II—patellae-tibiae and metatarsi striped yellow, with brown sides, tarsi yellow; rest of leg III—patella-tibia dark red-brown, with yellow-orange tarsus. Legs lightly hirsute. Tibia I ventral spination: 3–3, very long and moderately thin.

External epigynum with two small openings at lateral ends of a horizontal lip (Fig. 251). Internal structure with two globose spermathecae with wide necks extending posteriorly (Fig. 252).

Diagnosis. Myrmecotypus fuliginosus differs from *M. lineatipes* in its much smaller epigynal openings.

Natural history. Nothing is known of the habits of this species.

Distribution. Known only from its type locality in Tabasco, Mexico (Map 14).

Records. MEXICO. *Tabasco.*

Myrmecotypus lineatipes Chickering
Figures 249, 250. Map 14.

Myrmecotypus lineatipes Chickering, 1937, Trans. Amer. Microscop. Soc. 56(1):34–35, figs. 1, 32, ♀, from Barro Colorado Island, Panama Canal Zone; in the Museum of Comparative Zoology, examined.

FEMALE

Measurements. Based on one female holotype: carapace length 3.10 mm; carapace width 1.50 mm; carapace index 49; sternum length 1.30 mm; sternum width 0.75 mm; sternum index 58.

Femur IV length 2.30 mm; femur IV width 0.45 mm; leg thickness index 19; leg length index 73.

Abdomen length 3.20 mm; abdomen width 2.40 mm; abdomen index 75; dorsal sclerite length 0.85 mm; dorsal sclerite width 0.95 mm; dorsal sclerite index 115.

Description. Carapace brown-black with long, thin, white hairs. Eyes small and equal except the anterior median eyes almost twice the diameter of anterior laterals; both rows recurved when viewed dorsally, the posterior row one third wider than the anterior row. Carapace only slightly narrowed in head region (cephalic width index 79) and squarely truncated anteriorly. Thoracic groove absent with a slight depression in its place.

Abdomen short and wide, with a fairly small, brown-black dorsal sclerite. Abdomen covered with heavy yellowish pubescence and longer, sparser hairs. Ventral

abdomen with a dark red-brown epigastric sclerite. First pair of abdominal setae very thin, second pair moderately thin. Pedicel fairly short.

Sternum brown-black, elongate, and pinched slightly at coxa III, with very sparse, thin setae.

Chelicerae moderately brown-black, with two moderate teeth, the distal a bit smaller than the proximal one, and two promargin teeth, the distal one much larger and the proximal one slightly smaller than the retromargin teeth.

Coxa I moderately brown-black, IV dark brown-black, and II and III brilliant white. Trochanter IV notch absent.

Femora I and II striped, with a thin dorsal and partial lateral black-brown stripes on yellow-white ground, femora III and IV black-brown (somewhat lightened at distal end); patellae-tibiae I and II with lateral dark stripes, metatarsus I also striped, but II dark yellow; tarsi I and II yellow white; rest of III and IV gradually lightening from black-brown to red-brown, with patellae, distal end of tibiae and tarsi much lighter. Tibia I ventral spination: 3–3.

External epigynum with two fairly large flared openings (Fig. 250). Internal structure with somewhat globose spermathecae having posterior thin necks (Fig. 251).

Diagnosis. Myrmecotypus lineatipes differs from *M. fuliginosus* in its much larger epigynal openings.

Remarks. M. lineatipes is very closely related to *M. fuliginosus*, differing slightly in genitalia and size.

Natural history. Nothing is known of the habits of this species.

Distribution. Panama (Map 14).

Records. CANAL ZONE. Barro Colorado Island.

The *lineatus* Group

Myrmecotypus lineatus (Emerton), new combination Figures 111, 112, 153–155. Map 15.

Castianeira lineata Emerton, 1909, Trans. Connecticut Acad. Sci. 14(3):216, pl. 10, fig. 5, ♀, from Sharon, Massachusetts; in the Museum of Comparative Zoology, examined.

FEMALE

Measurements. Based on holotype and 6 females, holotype listed first, range of all follows: carapace length 2.70 mm, 2.35–2.75 mm; carapace width 1.40 mm, 1.20–1.40 mm; carapace index 52, 48–53; sternum length 1.20 mm, 1.05–1.25 mm; sternum width 0.70 mm, 0.70–0.75 mm; sternum index 55, 55–70.

Femur IV length 2.35 mm, 2.00–2.40 mm; femur IV width 0.30 mm, 0.30–0.35 mm; leg thickness index 14, 13–15; leg length index 87, 80–90.

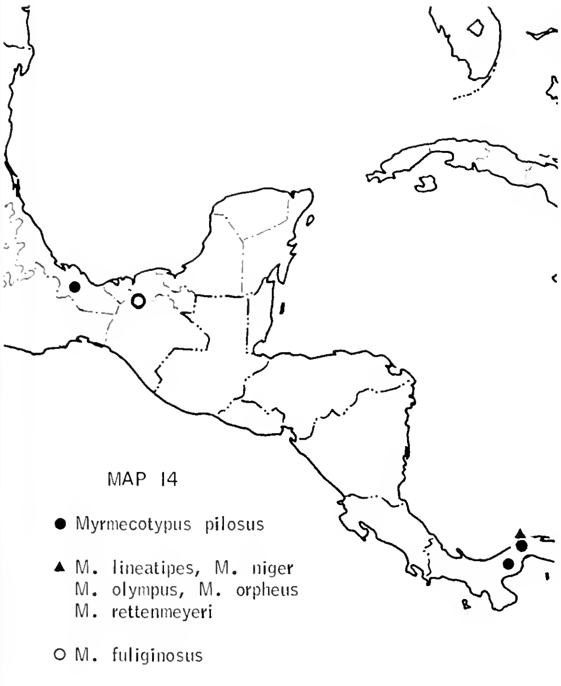
Abdomen length 2.85 mm, 2.85–3.60 mm; abdomen width 1.40 mm, 1.20–2.25 mm; abdomen index 49, 39–65; dorsal sclerite length 0.80 mm, 0.65–1.00 mm; dorsal sclerite width 0.60 mm, 0.50–0.60 mm; dorsal sclerite index 76, 58–76.

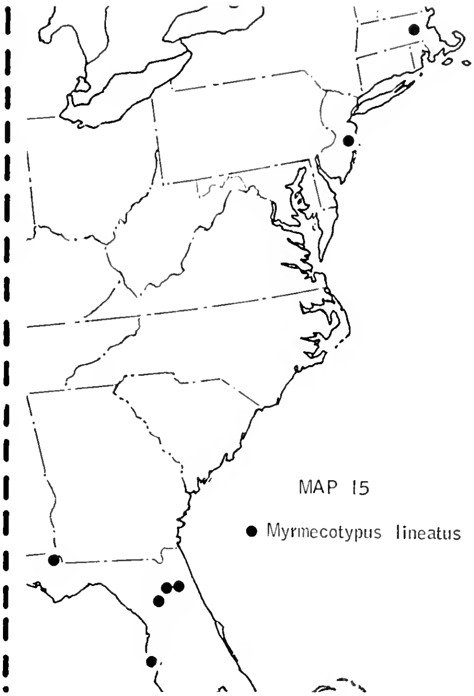
Description. Carapace yellow-orange, hairless and long, slightly darker in cephalic region. Cephalic region quite wide (cephalic width index 72–78) and truncated anteriorly. Eyes very small, equal (anterior median eyes slightly larger than anterior lateral eyes) and bordered in black (Fig. 153). Carapace narrows considerably behind, with posterior end raised slightly (Fig. 154). Thoracic groove absent, but a small longitudinal impression present.

Abdomen long oval, with a very strong median constriction and a moderate yellow dorsal sclerite. Two thin horizontal white hairs bands—one over the sclerite and one at constriction. Posterior third of abdomen dark purple-brown, with several pairs of light spots (Fig. 155). Epigastric sclerite light yellow. Ventrum creamy white. First pair of abdominal setae very thin and long, second pair moderate and fairly stout.

Sternum shield-shaped, long, light yellow, with a few long, very thin setae. Pedicel moderately long.

Chelicerae orange, with two moderately





small retromargin teeth and two promargin teeth, the distal larger and the proximal smaller than the retromargin teeth; an extremely small denticle just medial and distal to the larger promargin tooth. Several fairly thick, serrated setae at promargin chelicerae apex.

Coxa I light tan, II and III creamy white, IV yellow-white. Trochanter IV notch absent.

Legs very thin. Femora striped—I and II light yellow-white, with dark brown dorsal and prolateral stripes, III yellow, with dorsal and lateral red-brown stripes, IV dark yellow, with dorsal and retrolateral light red-brown stripes. Rest of legs I and II yellow-white; rest of leg III—patella-tibia yellow, slightly striped, metatarsus and tarsus light yellow; rest of leg IV—patella yellow, tibia striped like femur IV, metatarsus red-brown, tarsus creamy white. Legs lightly hirsute. Tibia I ventral spination: 2–2, thin and long.

External epigynum with two small circular openings (Fig. 112). Internal structure with rounded spermathecae and wide posterior necks (Fig. 111).

Diagnosis. Myrmecotypus lineatus differs from all other *Myrmecotypus* in its small eyes (Fig. 153), its tibia I ventral spination (2–2), and its abdominal shape and pattern (Fig. 155).

Remarks. This species is found along the eastern seaboard of the U.S. from Massachusetts to Florida. It is most abundant in Florida, which is probably the center of its distribution, with Massachusetts (the type locality) a peripheral area.

This atypical *Myrmecotypus* is not closely related to any other species.

Natural history. Nothing is known of the habits of this species.

Distribution. Massachusetts to Florida (Map 15).

Records. Florida. Alachua Co., Bradford Co., Clay Co., Jackson Co., Pinellas Co. *Massachusetts.* Norfolk Co., *New Jersey.* Ocean Co.

Myrmecotypus niger Chickering
Figures 241–244, 286. Map 14.

Myrmecotypus niger Chickering, 1937, Trans. Amer. Microscop. Soc. 56(1):35–37, figs. 42, 54, ♂, from Barro Colorado Island, Panama Canal Zone; in the Museum of Comparative Zoology, examined.

MALE

Measurements. Based on one male holotype: carapace length 2.45 mm; carapace width 1.10 mm; carapace index 46; sternum length 1.10 mm; sternum width 0.65 mm; sternum index 57.

Femur IV length 1.65 mm; femur IV width 0.35 mm; leg thickness index 20; leg length index 68.

Abdomen length 1.90 mm; abdomen width 1.35 mm; abdomen index 71.

Embolus length 0.08 mm; bulb length 0.75 mm; male genital index 11.

Description. Carapace dark reddish brown, with thin, long, white hair. A distinct, shallow, horizontal impression between the cephalic and thoracic regions. Eyes small and equal except the anterior median eyes almost twice the diameter of anterior laterals; both rows recurved when viewed dorsally, the posterior row one-half wider than the anterior row. Carapace only slightly narrowed in head region (cephalic width index 86) and squarely truncated anteriorly. Thoracic groove absent, with a depression in its place.

Abdomen short and rounded, with three-fourths full red-brown dorsal sclerite covered with fairly long white pubescence. Ventral abdomen with a red-brown epigastric sclerite, a square ventral sclerite posterior to the epigastric furrow, and a small inframammilliary sclerite. Abdominal setae very long—first pair very thin, second pair moderately thin. Short rugose petiole and a short pedicel.

Sternum deep maroon, with sparse, hair-like setae.

Chelicerae dark red-brown, with two moderately small retromargin teeth and two promargin teeth, the distal one much larger than, and the proximal one the same size as, the retromargin teeth. A very small denticle just distal and slightly median to the larger promargin tooth.

Coxa I light yellow-brown, II yellow-white, III and IV brown-black. Trochanter IV notch absent.

Leg I missing. Femora red-brown, darkening from II to IV. Patella-tibia and metatarsus II laterally striped with brown-black. Rest of legs III and IV red-brown. Legs lightly hirsute.

Pedipalp with no tibial apophysis. Tarsus with a globose genital bulb drawn out into a short neck with two sclerotized terminal structures—a straight embolus and a hooked conductor (Figs. 243, 244).

FEMALE

Measurements. Based on one female: carapace length 2.65 mm; carapace width 1.20 mm; carapace index 45; sternum length 1.15 mm; sternum width 0.60 mm; sternum index 50.

Femur IV length 1.80 mm; femur IV width 0.30 mm; leg thickness index 18; leg length index 68.

Abdomen length 2.05 mm; abdomen width 1.75 mm; abdomen index 87; dorsal sclerite length 1.45 mm; dorsal sclerite width 1.75 mm; dorsal sclerite index 122.

Description. Carapace dark maroon-brown with light, low pubescence. A distinct shallow impression between the cephalic and thoracic regions. Black hair bands starting at impression and running laterally and posteriorly (Fig. 286). Eyes small and equal except the anterior median eyes almost twice the diameter of anterior laterals, both rows recurved when viewed dorsally, the posterior row two-fifths wider than the anterior row. Carapace only slightly narrowed in cephalic region (cephalic width index 89) and squarely truncated anteriorly. Thoracic groove absent, with a distinct depression in its place.

Abdomen short and rounded with an almost three-fourths full, maroon-brown,

dorsal sclerite. Rest of dorsum and ventrum blackish. Epigastric and small inframammilliary sclerites red-brown.

Sternum deep maroon with sparse, hair-like setae.

Chelicerae dark red-brown, with two moderately small retromargin teeth and two promargin teeth, the distal one much larger than, and the proximal one the same size as, the retromargin teeth. A very small denticle just distal and slightly median to the larger promargin tooth.

Coxa I light yellow-brown, II yellow-white, III and IV brown-black. Trochanter IV notch absent.

Femur I basally yellow, distally white, with a thin ventral and a moderate dorsal red-brown stripe; femur II yellow with orange-brown sides; femora III and IV orange-brown. Rest of leg I—patella-tibia yellow-white with dark red-brown sides, metatarsus dark red-brown, tarsus creamy white; rest of leg II—patella-tibia and metatarsus yellow-white with red-brown sides, tarsus light yellow; rest of legs III and IV orange-brown, distal half of tarsi light yellow. Legs lightly hirsute. Tibia I ventral spination: 4–4, moderately long.

External epigynum with two flared openings (Fig. 242). Internal structure with long, globose spermathecae with thick necks and very thin bursae copulatrices (Fig. 241).

Diagnosis. Myrmecotypus niger differs from other *Myrmecotypus* in its wide cephalic region (male cephalic width index 86, female 89), male genitalia (with two pronged terminal processes on the genital bulb), female genitalia, and tibia I ventral spination (4–4).

Remarks. M. niger resembles *M. rettenmeyeri* in coxae color pattern and high values for the cephalic width index, but the genitalia are quite different.

Natural history. Nothing is known of the habits of this species.

Distribution. Panama (Map 14).

Records. CANAL ZONE. Barro Colorado Island, Summit.

THE *OLYMPUS* GROUP

Characteristics. Coxae I and II are white, other coxae much darker. Tibia I ventral spination 3–3. Male genital bulb with both loops lateral to the main palpal duct.

Myrmecotypus olympus new species

Figures 258–261, 289. Map 14.

Holotype. Male from Barro Colorado Island, Panama Canal Zone, 18-VII-1954 (A. M. Chickering); in the Museum of Comparative Zoology. The specific name is a noun in apposition after the mythical abode of the Greek gods.

MALE

Measurements. Based on one male holotype: carapace length 2.25 mm; carapace width 1.10 mm; carapace index 50; sternum length 0.95 mm; sternum width 0.60 mm; sternum index 60.

Femur IV length 1.65 mm; femur IV width 0.30 mm; leg thickness index 20; leg length index 73.

Abdomen length 1.75 mm; abdomen width 1.20 mm; abdomen index 70.

Genital bulb length 0.83 mm.

Description. Fairly small spider. Carapace with a very strong wide groove between the cephalic and thoracic region; orange-brown, with some short white pubescence. Eyes in two recurved rows, the posterior row about two-fifths wider than the anterior row; the posterior eyes moderately small and equal, the anterior medians larger and the anterior laterals smaller than the posterior eyes. Eyes bordered in black. Cephalic region narrower than the thoracic region (cephalic width index 72) and squarely truncated anteriorly. Thoracic groove absent.

Abdomen oval, with an almost full orange-brown sclerite and a thin yellow horizontal band. Epigastric and moderately large ventral sclerite light yellow-brown.

Moderately large brownish inframammilliary sclerite. First pair of abdominal setae very thin, second pair moderate.

Sternum shield-shaped and elongated, mottled brown and yellow, with some long, light hairs.

Chelicerae pale yellow-brown with two moderately small retromargin teeth and two promargin teeth, the distal larger and the proximal slightly smaller than the retromargin teeth; a moderately strong denticle medial and distal to the larger retromargin tooth.

Coxae I and II brilliant white, coxae III and IV pale yellow-brown. Trochanter IV notch absent.

Femora I and II striped creamy white, with a dark brown stripe on each side of dorsum; femora III and IV reddish brown (with ventrum and dorsum of III light yellow and base of IV yellow). Rest of I and II with striped patellae-tibiae and metatarsi (yellow-white with brown sides) and creamy white tarsi; rest of III and IV dark reddish yellow-brown, with white patella IV and light yellow-white tarsi. Legs moderately lightly hirsute. Tibia I ventral spination: 3–3, moderately thin and short.

Pedipalp with no tibial apophysis. Tarsus with a globose bulb drawn out into a short neck with a strong, curved embolus. Palpal ducts with two loops both lateral to the embolus tube (Fig. 260). A group of thick, heavy spines near the base of cymbium, near lateral edge (Fig. 261).

FEMALE

Measurements. Based on one female: carapace length 2.30 mm; carapace width 1.10 mm; carapace index 47; sternum length 1.00 mm; sternum width 0.60 mm; sternum index 61.

Femur IV length 1.65 mm; femur IV width 0.30 mm; leg thickness index 19; leg length index 72.

Abdomen length 2.20 mm; abdomen width 1.65 mm; abdomen index 75; dorsal sclerite length 1.50 mm; dorsal sclerite width 1.50 mm; dorsal sclerite index 100.

Description. Fairly small spider. Carapace with a very strong, wide groove between the cephalic and thoracic region. Cephalic region orange-brown and hairless, thoracic region red-brown with some long hairs, with some dark markings in the center. Eyes in two recurved rows, the posterior row about two-fifths wider than the anterior row; the posterior eyes moderately small and equal, the anterior medians larger and the anterior laterals smaller than the posterior eyes. Eyes bordered in black. Cephalic region narrower than the thoracic region (cephalic width index 81) and squarely truncated anteriorly. Thoracic groove absent.

Abdomen a wide oval, with a moderately large red-brown dorsal sclerite with a horizontal yellow stripe across it (Fig. 289). Rest of dorsum and ventrum brownish purple. Epigastric and small inframammilliary sclerites red-brown. First pair of abdominal setae very thin, second pair moderately thin.

Sternum shield-shaped and elongated, mottled brown and yellow, with some long, light hairs.

Chelicerae deep yellow, with two moderately small retromargin teeth and two promargin teeth, the distal larger and the proximal slightly smaller than the retromargin teeth; a strong denticle medial and distal to the larger retromargin tooth. About eight heavy, serrated setae at promarginal apex of each chelicerae.

Coxae I and II brilliant white, coxae III and IV dark yellow-brown. Trochanter IV notch absent.

Femora I and II striped creamy white, with a dark brown stripe on each side of dorsum; femora III and IV dark red-brown (slightly darker on sides). Rest of legs I and II with striped patellae-tibiae (light yellow with brown sides), red-brown metatarsi, yellow-white tarsi; rest of legs III and IV red-brown, with light yellow patella IV,

yellow-white tarsus III, and yellow-orange tarsus IV. Legs moderately lightly hirsute. Tibia I ventral spination: 3–3, moderately thin and very long.

External epigynum with two anteriorly directed semicircular openings (Fig. 258). Internal structure with bursae copulatrices running to globose spermathecae having wide necks (Fig. 259).

Diagnosis. Myrmecotypus olympus has a strong impression between the thoracic and cephalic regions, is orange-brown, and has distinctive male and female genitalia.

Remarks. This species is closely related to *M. orpheus*, and the male genitalia, with its double lateral loop and low twist, suggests a relationship with the highly modified *M. rettenmeyeri.*

Natural history. Nothing is known of the habits of this spider, but its general appearance is antlike, probably mimicking some small formicine ants.

Distribution. Panama (Map 14).

Records. CANAL ZONE. Barro Colorado Island.

Myrmecotypus orpheus new species

Figures 253–257, 288. Map 14.

Holotype. Male from Summit Gardens, Panama Canal Zone, 12-V-1964 (A. M. Chickering); in the Museum of Comparative Zoology. The specific name is a noun in apposition after the mythical Greek lover Orpheus.

MALE

Measurements. Based on holotype and one male, holotype listed first, range of both follows: carapace length 1.75 mm, 1.75–1.95 mm; carapace width 0.90 mm, 0.90–0.95 mm; carapace index 51, 48–51; sternum length 0.75 mm, 0.75–0.80 mm; sternum width 0.45 mm, 0.45 mm; sternum index 63, 56–63.

Femur IV length 1.30 mm, 1.30–1.40 mm; femur IV width 0.25 mm, 0.25 mm; leg thickness index 20, 19–20; leg length index 75, 71–75.

Abdomen length 1.50 mm, 1.40–1.50 mm; abdomen width 1.10 mm, 0.95–1.10 mm; abdomen index 72, 67–72.

Embolus length 0.03 mm, 0.03 mm; bulb length 0.44 mm, 0.44–0.51 mm; male genital index 7, 6–7.

Description. Fairly small spider. Carapace shiny reddish brown-black, with a deep groove between the cephalic and thoracic regions, reinforced on the sides with some white hairs, and very sparse white hairs elsewhere. Eyes in two recurved rows, the posterior row about two-fifths wider than the anterior row; the posterior eyes moderately small and equal, the anterior medians larger and the anterior laterals smaller than the posterior eyes. Cephalic region narrower than the thoracic region (cephalic width index 75–79) and squarely truncated anteriorly. Thoracic groove absent.

Abdomen a wide oval, with a four-fifths full, shiny, dark red-brown dorsal sclerite with a few light hairs. Epigastric, ventral (one-half) and small inframammilliary sclerites yellow-brown. First pair of abdominal setae extremely thin, second pair very thin.

Sternum shield-shaped and elongated, dark red-brown, with some long, light hairs.

Chelicerae yellow-brown, with two moderately small retromargin teeth and two promargin teeth, the distal larger and the proximal slightly smaller than the retromargin teeth; a strong denticle medial and distal to the larger retromargin tooth.

Coxae I and II white, coxae III and IV brown-black. Trochanter IV notch absent.

Femora I and II white, I with brown-black spot at prolateral base, II with prolateral brown-black stripe; femora III and IV dark brown-black (IV with a white base). Rest of legs I and II—both patellae-tibiae and metatarsus II light yellow with brown sides, metatarsus I dark red-brown, tarsi creamy white; rest of legs III and IV brown-black, with white patella IV and

white tarsi. Legs lightly hirsute. Tibia I ventral spination: 3–3, moderate.

Pedipalp with no tibial apophysis. Tarsus small, with a globose bulb drawn out into a short, wide neck with a short, pointed embolus (Figs. 255–257). Reservoir tubes with two loops, both lateral to the embolus tube.

FEMALE

Measurements. Based on 2 females: carapace length 2.25–2.30 mm; carapace width 1.05–1.10 mm; carapace index 47–49; sternum length 1.00 mm; sternum width 0.60 mm; sternum index 61.

Femur IV length 1.60–1.65 mm; femur IV width 0.30 mm; leg thickness index 18; leg length index 72.

Abdomen length 2.05–2.20 mm; abdomen width 1.60–1.70 mm; abdomen index 78; dorsal sclerite length 1.45–1.50 mm; dorsal sclerlite width 1.50–1.60 mm; dorsal sclerite index 104.

Description. Fairly small spider. Carapace shiny reddish brown-black with a deep groove between the cephalic and thoracic regions, reinforced on the sides with some white hairs, and very sparse white hairs elsewhere (Fig. 288). Eyes in two recurved rows, the posterior row about two-fifths wider than the anterior row; the posterior eyes moderately small and equal, the anterior medians larger and the anterior laterals smaller than the posterior eyes. Cephalic region narrower than the thoracic region (cephalic width index 74–76) and squarely truncated anteriorly. Thoracic groove absent.

Abdomen a wide oval, with a three-quarters full, shiny, very dark red-brown dorsal sclerite with a faint, horizontal red-brown band. Rest of dorsum and ventrum purplish brown. Epigastric and small inframammilliary sclerite dark red-brown. First pair of abdominal setae extremely thin, second pair very thin.

Sternum shield-shaped and elongated, dark red-brown with some light, long hairs.

Chelicerae red-brown, with two moderately small retromargin teeth and two promargin teeth, the distal larger and the proximal slightly smaller than the retromargin teeth; a strong denticle medial and distal to the larger retromargin tooth. About eight heavy, serrated setae at promarginal apex of each chelicerae.

Coxae I and II white, coxae III and IV brown-black. Trochanter IV notch absent.

Femora I and II yellow-white, I with dark brown retrolateral dorsal stripe, II with retro- and prolateral stripes; femora III and IV dark reddish brown-black. Rest of legs I and II—patellae-tibiae and metatarsi light yellow with sides brown, tarsi yellow-white; rest of legs III and IV dark reddish brown-black with light whitish patella IV and light yellow tarsi. Legs lightly hirsute. Tibia I ventral spination: 3–3, moderately long and strong.

External epigynum with two anteriorly directed, semi-circular openings (Fig. 258). Internal structure with bursae copulatrices running to globose spermathecae with wide necks (Fig. 259).

Diagnosis. Myrmecotypus orpheus has a strong impression between thoracic and cephalic regions, is dark brown-black, and has distinctive male and female genitalia.

Remarks. (See *Remarks* under *M. olympus.*)

Natural history. Nothing is known of the habits of this spider, but its general appearance is antlike, probably mimicking some small formicine ant.

Distribution. Panama (Map 14).

Records. CANAL ZONE. Barro Colorado Island, Forest Reserve, Summit.

Myrmecotypus rettenmeyeri Unzicker
Figures 262–265, 287. Map 14.

Myrmecotypus rettenmeyeri Unzicker, 1965, J. Kansas Entomol. Soc. 38(3):253–256, figs. 1, 2 ♂, from Barro Colorado Island, Panama Canal Zone; in the Kansas State University Museum, examined. Reiskind, 1966, Psyche 72(4)"1965": 279–281, fig. 1.

Myrmecotypus discreta Unzicker, 1965, J. Kansas Entomol. Soc. 38(3):256–257, figs. 3, 4, ♀, from Barro Colorado Island, Panama Canal Zone; in the Kansas State University Museum, examined.

MALE

Measurements. Based on one male: carapace length 5.15 mm; carapace width 2.05 mm; carapace index 39; sternum length 2.40 mm; sternum width 0.95 mm; sternum index 39.

Femur IV length 4.50 mm; femur IV width 0.65 mm; leg thickness index 14; leg length index 88.

Abdomen length 3.65 mm; abdomen width 2.40 mm; abdomen index 66.

Description. A large spider. Carapace long and narrow, deep maroon-brown, with a weak horizontal impression between the cephalic and thoracic regions, and covered with low hairs, with white hair on posterior side of the impression and a band of black hairs just behind the white, off to the sides; a longitudinal band of erect black hairs down back of thoracic region (Fig. 287). Eyes small and equal, except anterior median eyes about two times the diameter of anterior lateral eyes. Both rows of eyes recurved, posterior row about one-third wider than anterior row. Thoracic groove absent. Cephalic region narrower than thoracic region (cephalic width index 76).

Abdomen oval (wider posteriorly), with a seven-eights full, maroon-brown dorsal sclerite, with long silvery hair and two thin horizontal black bands. Epigastric, ventral (almost full), and inframammilliary sclerites orange-brown. First pair of abdominal setae moderately thin and long, second moderately thick and long.

Sternum very elongated, brown-black, with very long thin hairs.

Chelicerae dark red-brown, with two moderately small retromargin teeth and three promargin teeth—the median larger, the proximal the same size, and the distal (medial and distal to the median promargin tooth) much smaller than the retromargin teeth.

Coxae I and II brilliant white, III and IV maroon-brown. Trochanter IV notch extremely small.

Femur I with dark brown basal half, apical half white with a wide dorsal and a pair of ventral brown stripes extending from basal section; femora II, III, and IV maroon-brown. Rest of legs I and II—patellae-tibiae yellow, with a pair of dorsal-lateral red-brown stripes (and patella-tibia I completely red-brown distally), metatarsi red-brown proximally and yellow-brown distally, yellow-brown tarsi (leg II somewhat darker); rest of legs III and IV brown-black, with proximal half of patella yellow-white and tarsi orange-brown. Legs moderately hirsute. Heavy hairs on tibiae III and IV, as in female. Tibia I ventral spination: 3–3, moderately long and thin.

Pedipalp with no tibial apophysis. Tarsus with a globose genital bulb drawn out into a thick neck with a small pointed embolus at the end of a large spiral twist (Figs. 262, 263).

FEMALE

Measurements. Based on 3 females: carapace length 5.25–5.75 mm; carapace width 2.05–2.20 mm; carapace index 38–39; sternum length 2.55–2.65 mm; sternum width 1.05 mm; sternum index 39–41.

Femur IV length 4.50–5.25 mm; femur IV width 0.60–0.70 mm; leg thickness index 13–14; leg length index 86–91.

Abdomen length 3.05–4.05 mm; abdomen width 2.15–3.55 mm; abdomen index 69–87; dorsal sclerite length 1.15–1.40 mm; dorsal sclerite width 1.05–1.15 mm; dorsal sclerite index 79–92.

Description. A large spider. Carapace long and narrow, dark orange-brown (darker in thoracic section), with a weak horizontal impression between the cephalic and thoracic regions, and covered with low hairs—white hair on posterior side of the

impression, a band of black hairs just behind the white, off to the sides, and a longitudinal band of erect black hairs down back of thoracic region. Eyes small and equal, except anterior median eyes about twice the diameter of anterior lateral eyes. Both rows of eyes recurved, the posterior row about one-third wider than anterior row. Thoracic groove absent. Cephalic region narrower than thoracic region (cephalic width index 81–87).

Abdomen a short oval, pointed posteriorly, with a moderately small, red-brown dorsal sclerite, and covered with long, silver hairs with three dark, thin, horizontal bands, the anterior one incomplete. Epigastric and small inframammilliary sclerites yellow-brown. Ventrum greyish brown, with a pair of light stripes from each side of epigastric furrow to region of posterior sclerite. First pair of abdominal setae thin, second pair moderate and long.

Sternum very elongated, brown-black, with very long, thin hairs.

Chelicerae red-brown, with two moderately small retromargin teeth and three promargin teeth—the median larger, the proximal the same size, and the distal (medial and distal to the median promargin tooth) much smaller than the retromargin teeth.

Coxae I and II brilliant white; III and IV brown-black. Only a trace of a trochanter IV notch.

Femur I with a brown-black basal half, apical half white with a wide dorsal and a pair of ventral brown-black stripes extending from basal section; femora II, III, and IV brown-black. Rest of legs I and II—patellae-tibiae yellow, with a pair of dorsal-lateral red-brown stripes (and patella-tibia I completely red-brown distally), metatarsi red-brown proximally and yellow-brown distally, yellow-brown tarsi (leg II somewhat darker); rest of legs III and IV brown-black, with proximal half of patella yellow-white and tarsi orange-brown. Legs moderately hirsute. Tibiae III and IV heavily hirsute, with heavy hairs, especially on dorsal sides. These hairs increase the apparent width of the distal end of tibia IV from 0.46 mm to 0.73 mm. Tibia I ventral spination: 3–3, very long and thin.

External epigynum with a horizontal, sclerotized lip and two lateral openings (Fig. 265). Internal structure with large, moderately globose spermathecae having wide necks and direct, moderate bursae copulatrices (Fig. 264).

Diagnosis. Myrmecotypus rettenmeyeri differs from all other *Myrmecotypus* in its large size and in the longitudinal row of dense hairs on the posterior of the thoracic region.

Remarks. The large size, thin legs, and strange hair growth on the carapace are the result of strong selection for a mimetic resemblance to *Camponotus sericeiventris* (Guérin). The female genitalia are similar to those of *M. niger*, but the male genitalia are very distinct, with the looping of the palpal duct more like that of the *olympus* group.

Natural history. This species mimics *Camponotus sericeiventris* and is found in the same habitat as that ant on Barro Colorado Island (Reiskind, 1966).

Distribution. Panama (Map 14).

Records. CANAL ZONE. Barro Colorado Island, Forest Reserve.

THE *PILOSUS* GROUP

Myrmecotypus pilosus (O. P.-Cambridge) Figures 245–248. Map 14.

Corinnomma pilosa O. P.-Cambridge, 1898, Biol. Centrali-Americana Arachnida 1:277–278, pl. 33, figs. 3, 4, ♂, ♀. Female holotype from Teapa, Tabasco, Mexico; in the British Museum (Natural History), examined.

Myrmecotypus pilosus: F. P.-Cambridge, 1894, Biol. Centrali-Americana Arachnida 2:84.

Myrmecotypus obscurus Chickering, 1937, Trans. Amer. Microscop. Soc. 56(1):37–38, figs. 18, 43, 80, ♂, ♀. Male holotype from Barro Colorado Island, Panama Canal Zone; in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

MALE

Measurements. Based on 10 males: carapace length 2.30–2.60 mm; carapace width 1.20–1.30 mm; carapace index 51–53; sternum length 1.05–1.15 mm; sternum width 0.60–0.70 mm; sternum index 58–69.

Femur IV length 1.65–1.75 mm; femur IV width 0.30–0.40 mm; leg thickness index 20–23; leg length index 65–72.

Abdomen length 2.05–2.40 mm; abdomen width 1.35–1.55 mm, abdomen index 64–68.

Embolus length 0.12–0.15 mm; bulb length 0.65–0.73 mm; male genital index 17–20.

Description. Carapace orange-brown, with a shallow impression between the cephalic and thoracic regions, and covered with moderately light white hairs, with some black hairs in the impression. Eyes small and equal, except the anterior median eyes twice the diameter of the anterior laterals, both rows recurved when viewed dorsally, the posterior row one-third wider than the anterior row. Carapace somewhat narrowed in head region (cephalic width index 65–72) and squarely truncated anteriorly. Thoracic groove absent.

Abdomen wide oval, with a full, red-brown dorsal sclerite covered with short white hairs and long erect hairs and with two horizontal bands of golden-brown hairs. Yellow-brown epigastric, ventral (almost full), and inframammilliary (small) sclerites. Abdominal setae extremely long—first pair thin, second pair moderate.

Sternum reddish brown, elongate, with long, light hairs.

Chelicerae yellow-brown, with two moderate retromargin teeth and three promargin teeth, the median one larger, the proximal one smaller, and the distal one much smaller than the retromargin teeth.

Coxa I light brown, II creamy white, III and IV yellow-brown. Trochanter IV notch absent.

Femur I yellow-white, with light brown stripes (dorsal and ventral) and base; femur II yellow-white, light brown on sides; femora III and IV light red-brown. Rest of I and II yellow-white—patellae-tibiae and metatarsi with red-brown sides (metatarsus I all red-brown); rest of III and IV light reddish brown (lightening distally to light orange-brown tarsi). Legs moderately lightly hirsute. Tibia I ventral spination: 3–3, moderately short and thin.

Pedipalp with no tibial apophysis. Tarsus with a globose genital bulb drawn out into a neck with a strong, spiral, simple embolus (Fig. 248). Bulb with an embolus palpal duct and a single loop in the basal globe (Fig. 247).

FEMALE

Measurements. Based on holotype and 8 females, holotype listed first, range of all follows: carapace length 2.95 mm, 2.50–2.95 mm; carapace width 1.50 mm, 1.30–1.50 mm; carapace index 50, 50–53; sternum length 1.30 mm, 1.10–1.30 mm; sternum width 0.75 mm, 0.65–0.75 mm; sternum index 56, 56–63.

Femur IV length 1.95 mm, 1.75–1.95 mm; femur IV width 0.40 mm, 0.35–0.40 mm; leg thickness index 22, 19–22; leg length index 65, 65–72.

Abdomen length 2.95 mm, 2.25–2.95 mm; abdomen width 2.20 mm, 1.75–2.40 mm; abdomen index 76, 72–90. Based on 8 females only, type measurements not included: dorsal sclerite length 1.45–1.90 mm; dorsal sclerite width 1.75–2.05 mm; dorsal sclerite index 97–127.

Description. Carapace dark red-brown, with a shallow impression between the cephalic and thoracic regions, covered with moderately light, white hairs. Eyes small and equal, except the anterior median eyes twice the diameter of anterior laterals, both rows recurved when viewed dorsally, the posterior row about one-fourth wider than the anterior row. Carapace somewhat narrowed in head region (cephalic width index 67–74) and squarely truncated anteriorly. Thoracic groove absent.

Abdomen a large oval, with a large, dark red-brown dorsal sclerite (about three-fifths length of abdomen), thick, low, white hairs and long, thin, erect hairs (more numerous on posterior half). A horizontal golden brown hair band on sclerite (broken in middle). Deep red-brown epigastric and small inframammilliary sclerites. Ventrum dull brown. Abdominal setae extremely long—first pair thin, second pair moderate.

Sternum dark red-brown, elongate, with long, light hairs.

Chelicerae red-brown, with two moderate retromargin teeth and three promargin teeth, the median one larger, the proximal one smaller, and the distal one much smaller than the retromargin teeth.

Coxa I light yellow-brown, II yellow-white, III dark yellow-brown, IV dark red-brown. Trochanter IV notch absent.

Femur I light yellow, with dark red-brown dorsal stripe and prolateral base; femur II light yellow-brown, with light red-brown sides; femora III and IV red-brown. Rest of legs I and II yellow, patellae-tibiae and metatarsi with red-brown sides, orange tarsi; rest of legs III and IV reddish brown, lighter tarsi. Legs moderately lightly hirsute. Tibia I ventral spination: 3–3, long and moderately thin.

External epigynum a wide slit (Fig. 245). Internal structure with two small, globose spermathecae with very short, small posterior necks (Fig. 246).

Diagnosis. Myrmecotypus pilosus differs from other *Myrmecotypus* species in its narrower cephalic region (cephalic width index 64–74) and distinctive genitalia.

Remarks. The male genitalia is very different from the genitalia of any other New World species of Castianeirinae and suggests a possible relationship with some Old World groups, e.g., *Corinnomma*, because of the single lateral loop in the globe of the genital bulb.

Natural history. O. P.-Cambridge (1898) quotes observations of the collector of the type specimen: "Female in a leaf, in thick woods near a stream; it was sitting on the point of the leaf with the front legs extended. A black ant resembling this spider is common in the same woods. According to my observations, these ant-like spiders eat only the species of ant which they resemble. A specimen of this spider was found in a shady glen." No other ant-mimicking clubionid has been observed eating ants, and this report should be confirmed.

Distribution. Mexico, Panama (Map 14).

Records. MEXICO. *Tabasco, Veracruz.*

PANAMA. El Valle.

CANAL ZONE. Barro Colorado Island, Experimental Gardens, Madden Dam.

Sphecotypus O. P.-Cambridge

Sphecotypus O. P.-Cambridge, 1895, Biol. Centrali-Americana Arachnida 1:152–153, pl. 19, fig. 4, ♀. Type species by monotypy: *Sphecotypus niger* (Perty).

Sphecotypus niger (Perty)
Figure 290.

Myrmecia nigra Perty, 1833, Delectus Animalium (ed. J. B. de Spix and F. P. Martius). Monachii, 1833:199, Pl. 39, Fig. 9, ♀, from Sebatianopolin (Rio de Janeiro), Brazil. C. L. Koch, 1842, Die Arachniden 9:15–17, ♀, Fig. 701.

Myrmecia niger: Keyserling, 1891, Spinn. Amer. 3 (Bras. Spinn.):80, pl. 2, fig. 40, ♀.

Sphecotypus formicarius O. P.-Cambridge, 1895, Biol. Centrali-Americana Arachnida 1:153, pl. 19, fig. 4, ♀, from Bugaba in Chiriqui, Panama; in the British Museum (Natural History).

Sphecotypus niger: Simon, 1897, Histoire Naturelle des Araignées 2(1):176, figs. 168, 169, 171, ♀. F. P.-Cambridge, 1899, Biol. Centrali-Americana Arachnida 2:84.

Diagnosis. Sphecotypus differs from all other Castianeirinae in its elongated carapace, constricted between the cephalic and thoracic regions with no further constrictions in the thoracic region (as in *Myrmecium*) (Fig. 290).

Remarks. This South American genus is monotypic, with its one species occurring in Panama. Proper classification of this species should await a study of the South American fauna, and therefore is only briefly noted here.

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Plate I

Figs. 7–10. *Castianeira longipalpus* (Hentz). 7, Internal epigynum, dorsal view. 8, External epigynum. 9, Left palpus. 10, Embolus.

Figs. 11–14. *Castianeira luctifera* Petrunkevitch. 11, Internal epigynum, dorsal view. 12, External epigynum. 13, Left palpus. 14, Embolus.

Figs. 15–18. *Castianeira alata* Muma. 15, Internal epigynum, dorsal view. 16, External epigynum. 17, Left palpus. 18, Embolus.

(Scale line for epigyna and palpi = 0.59 mm; for emboli = 0.15 mm.)

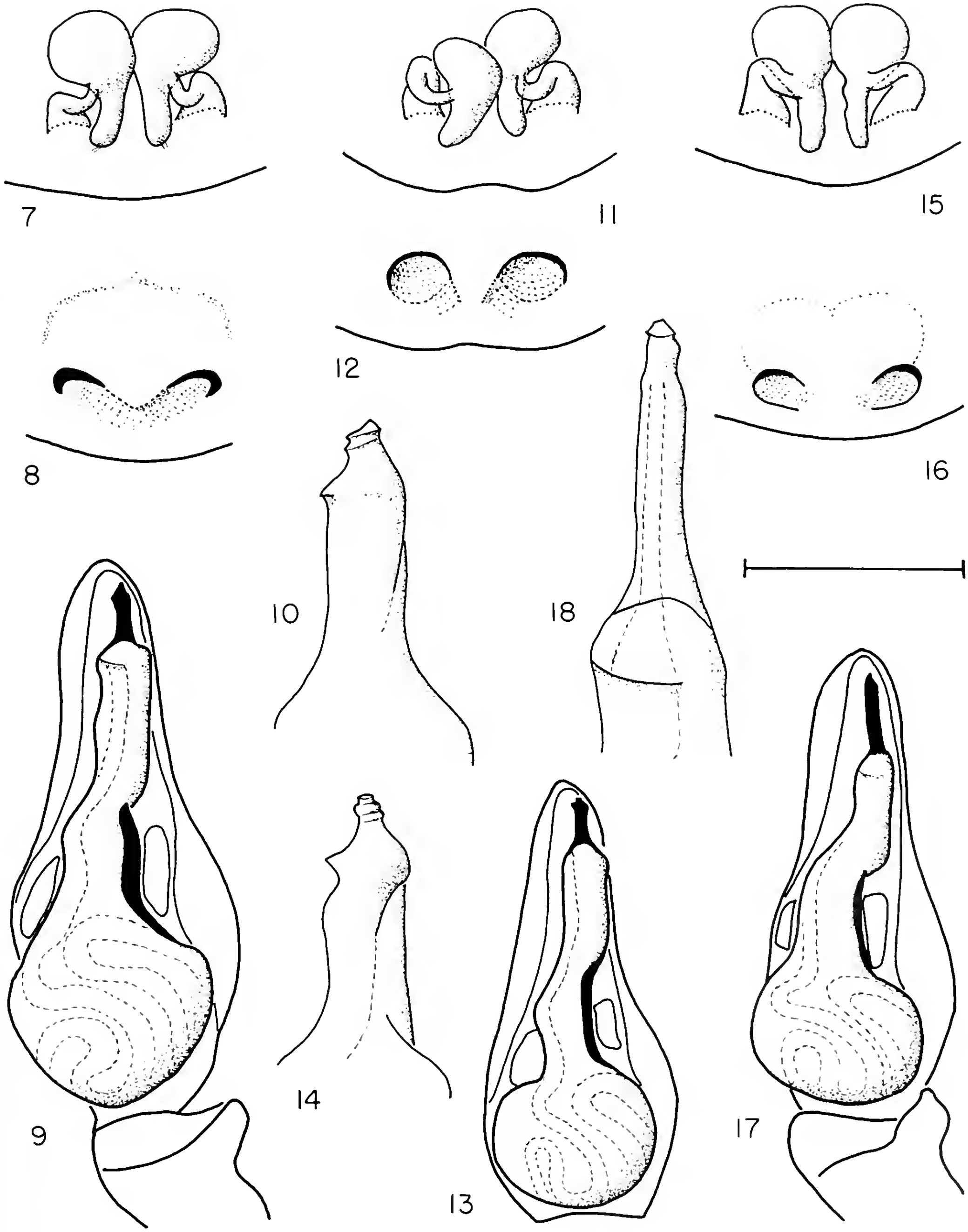
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Plate II

Figs. 19–23. *Castianeira variata* Gertsch. 19, Internal epigynum, dorsal view (Louisiana). 20, External epigynum (Louisiana). 21, Internal epigynum, dorsal view (Arkansas). 22, Left palpus. 23, Embolus.

Figs. 24–27. *Castianeira plorans* (O. P.-Cambridge). 24, External epigynum. 25, Internal epigynum, dorsal view. 26, Left palpus. 27, Embolus.

Figs. 28–31. *Castianeira thalia* n. sp. 28, Internal epigynum, dorsal view. 29, External epigynum. 30, Left palpus. 31, Embolus.

(Scale line for epigyna and palpi = 0.59 mm; for emboli = 0.15 mm.)

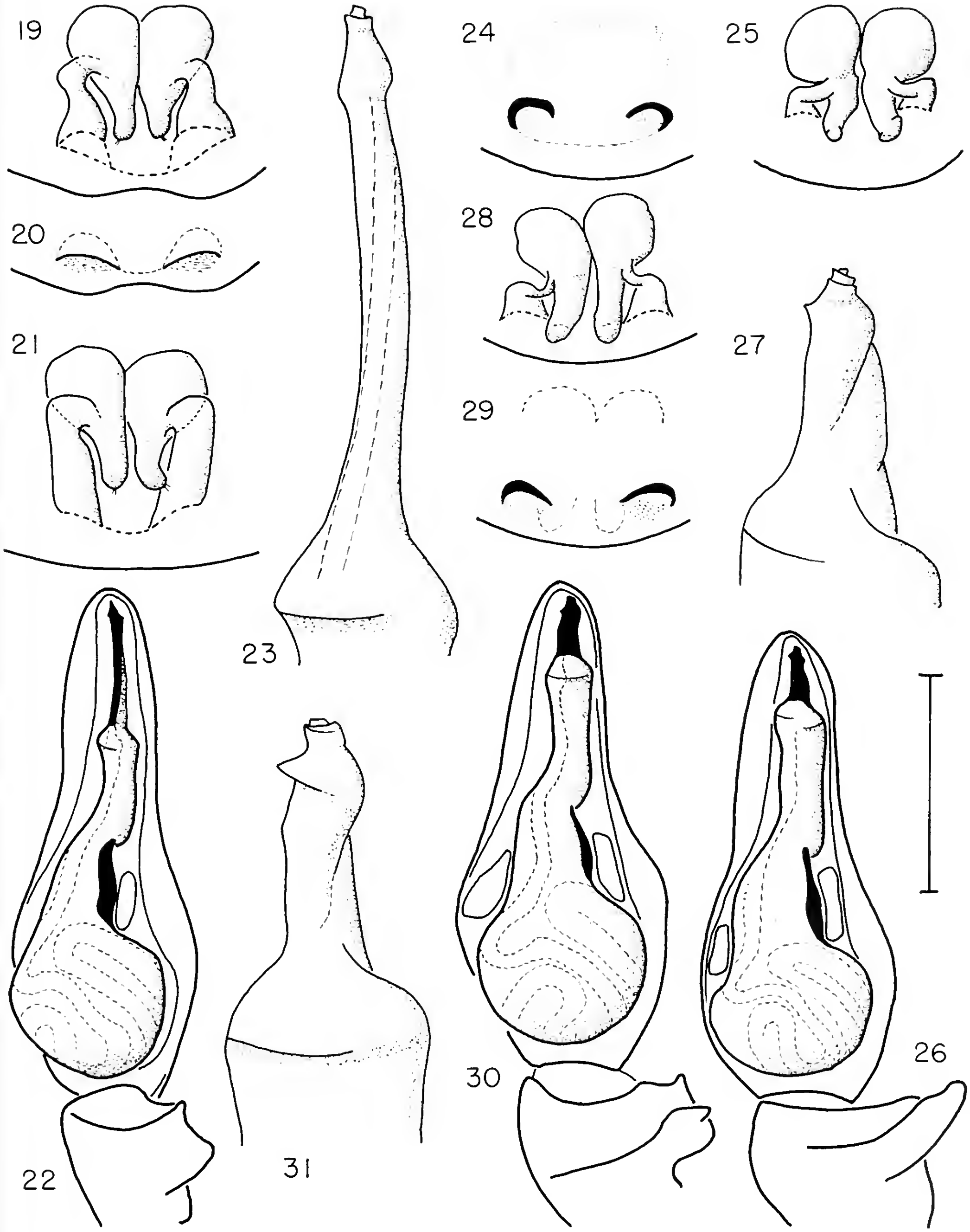
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Plate III

Figs. 32, 33. *Castianeira mexicana* (Banks). 32, Internal epigynum, dorsal view. 33, External epigynum.

Figs. 34, 35. *Castianeira lachrymosa* (O. P.-Cambridge). 34, Epigynum, ventral view cleared. 35, External epigynum.

Figs. 36, 37. *Castianeira venusta* (Banks). 36, Epigynum, ventral view cleared. 37, External epigynum.

Figs. 38, 39. *Castianeira flebilis* O. P.-Cambridge. 38, Internal epigynum, dorsal view. 39, External epigynum.

Figs. 40–43. *Castianeira floridana* (Banks). 40, Internal epigynum, dorsal view. 41, External epigynum. 42, Left palpus. 43, Embolus.

Figs. 44, 45. *Castianeira crocata* (Hentz). 44, External epigynum. 45, Internal epigynum, dorsal view.

Figs. 46–49. *Castianeira vulnerea* Gertsch. 46, External epigynum. 47, Internal epigynum, dorsal view. 48, Left palpus. 49, Embolus.

(Scale line for epigyna and palpi = 0.59 mm; for emboli = 0.15 mm.)

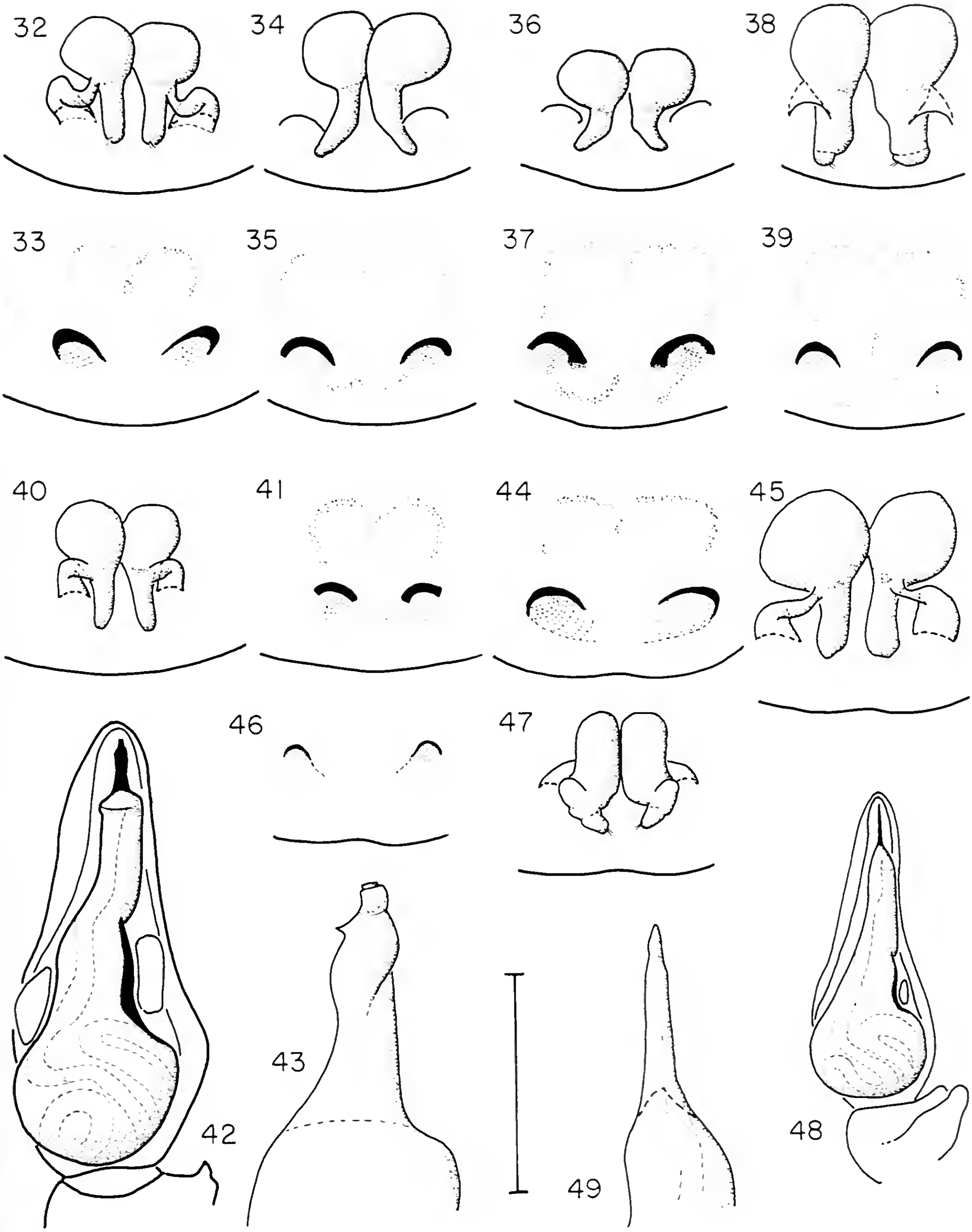
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Plate IV

Figs. 50–53. *Castianeira longipalpus* (Hentz). 50, Male abdomen. 51, Female abdomen. 52, Eye region of female. 53, Female carapace.

Figs. 54, 55. *Castianeira luctifera* Petrunkevitch. 54, Female abdomen. 55, Male abdomen.

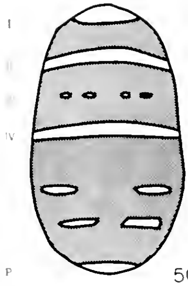
Fig. 56. *Castianeira crocata* (Hentz). Female abdomen.

Fig. 57. *Castianeira venusta* (Banks). Female abdomen.

Figs. 58, 59. *Castianeira floridana* (Banks). 58, Female abdomen. 59, Male abdomen.

Figs. 60, 61. *Castianeira variata* Gertsch. 60, Male abdomen. 61, Female abdomen.

(Scale line for abdomens and carapaces = 2.72 mm; for eye region = 0.94 mm.)



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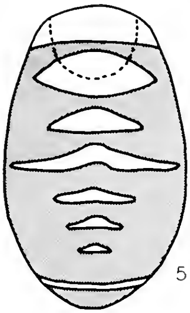

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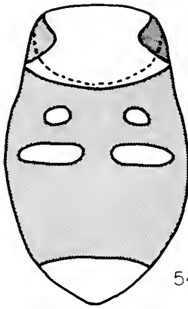

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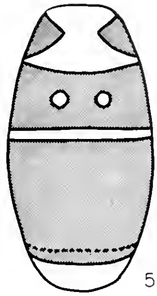

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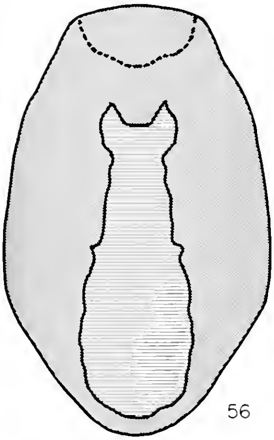

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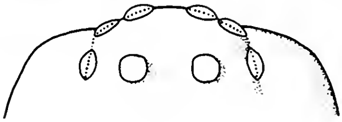

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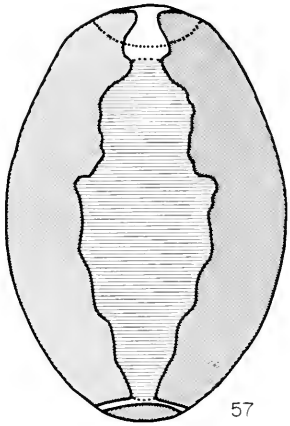

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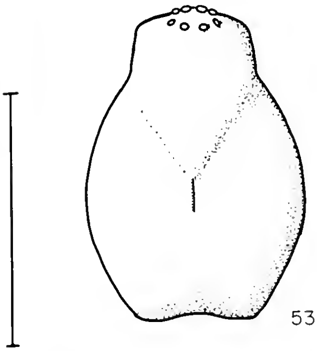

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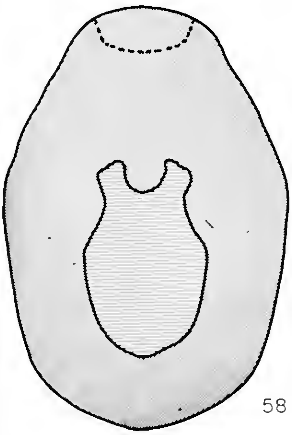

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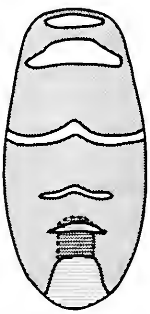

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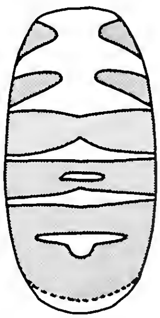

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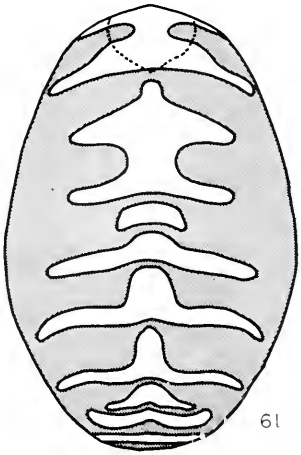

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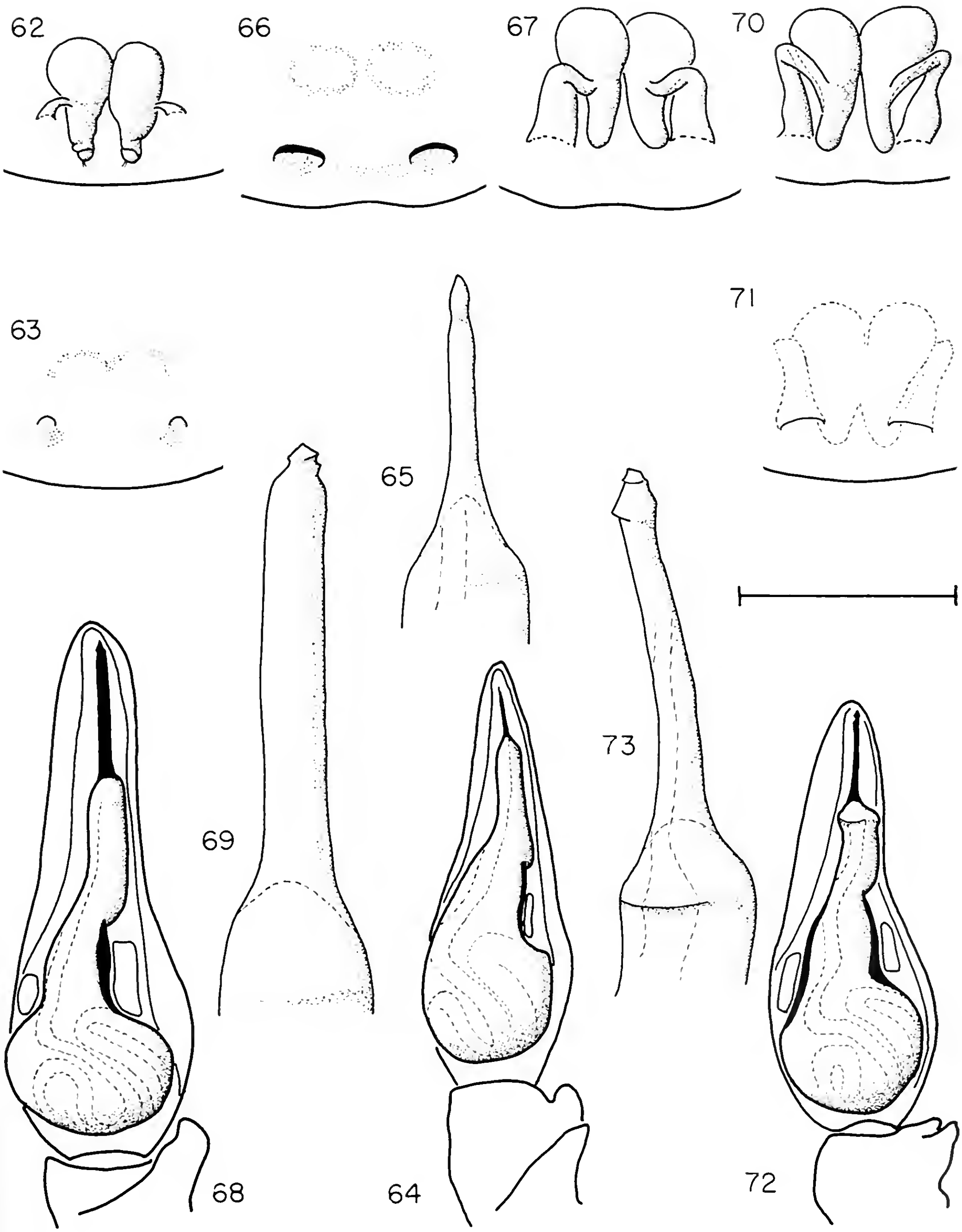
(Scale line for epigyna and palpi = 0.59 mm; for emboli = 0.15 mm.)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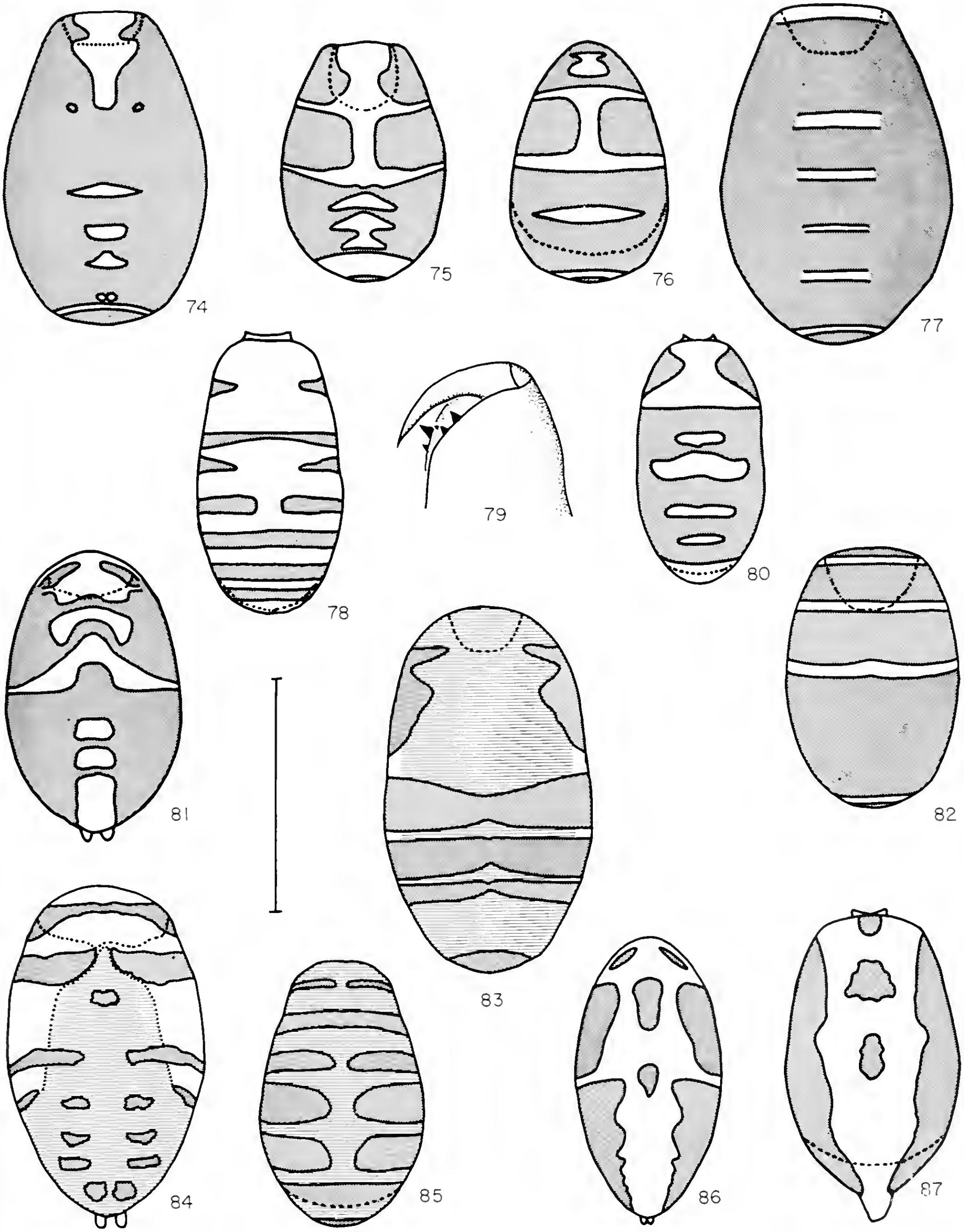
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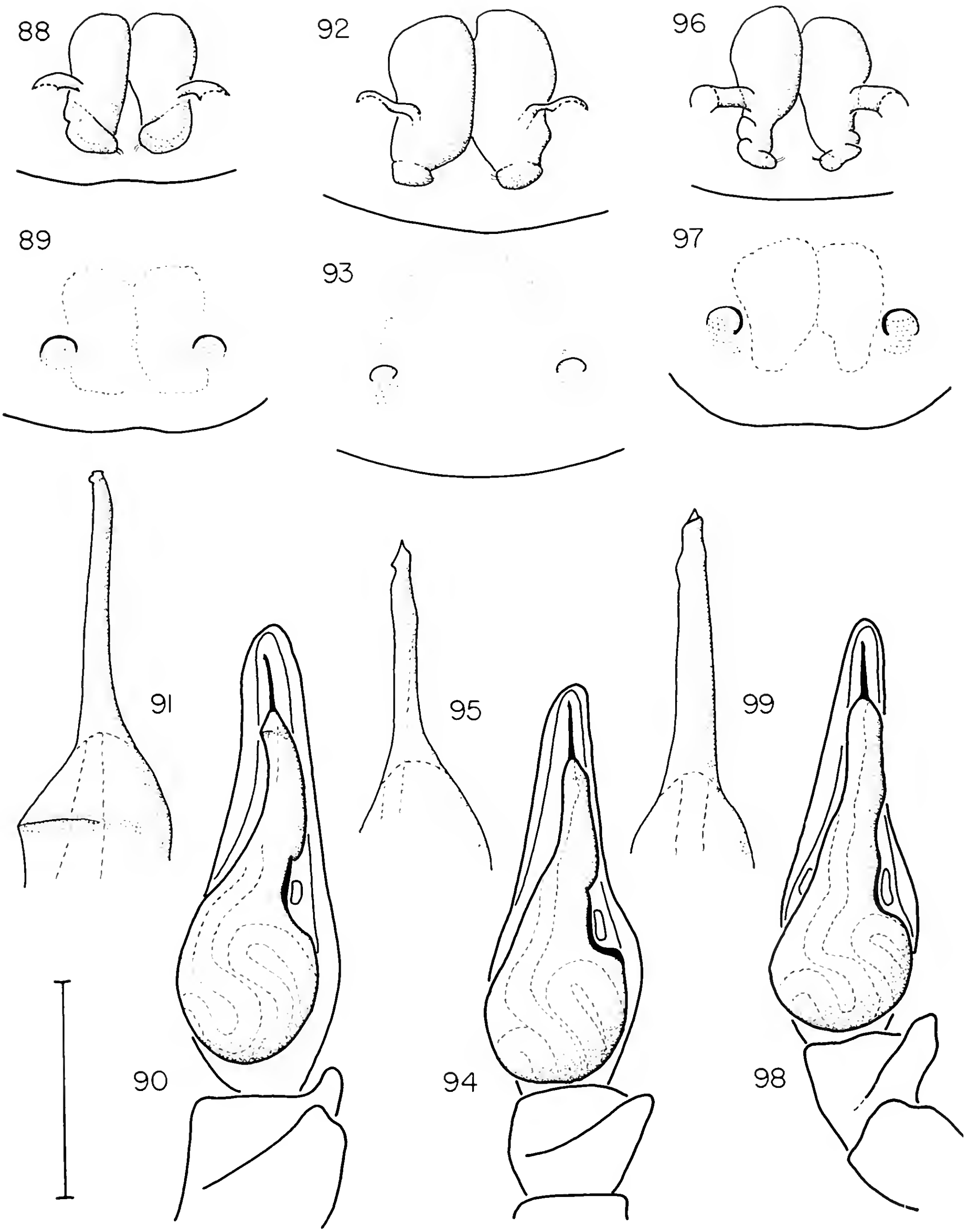
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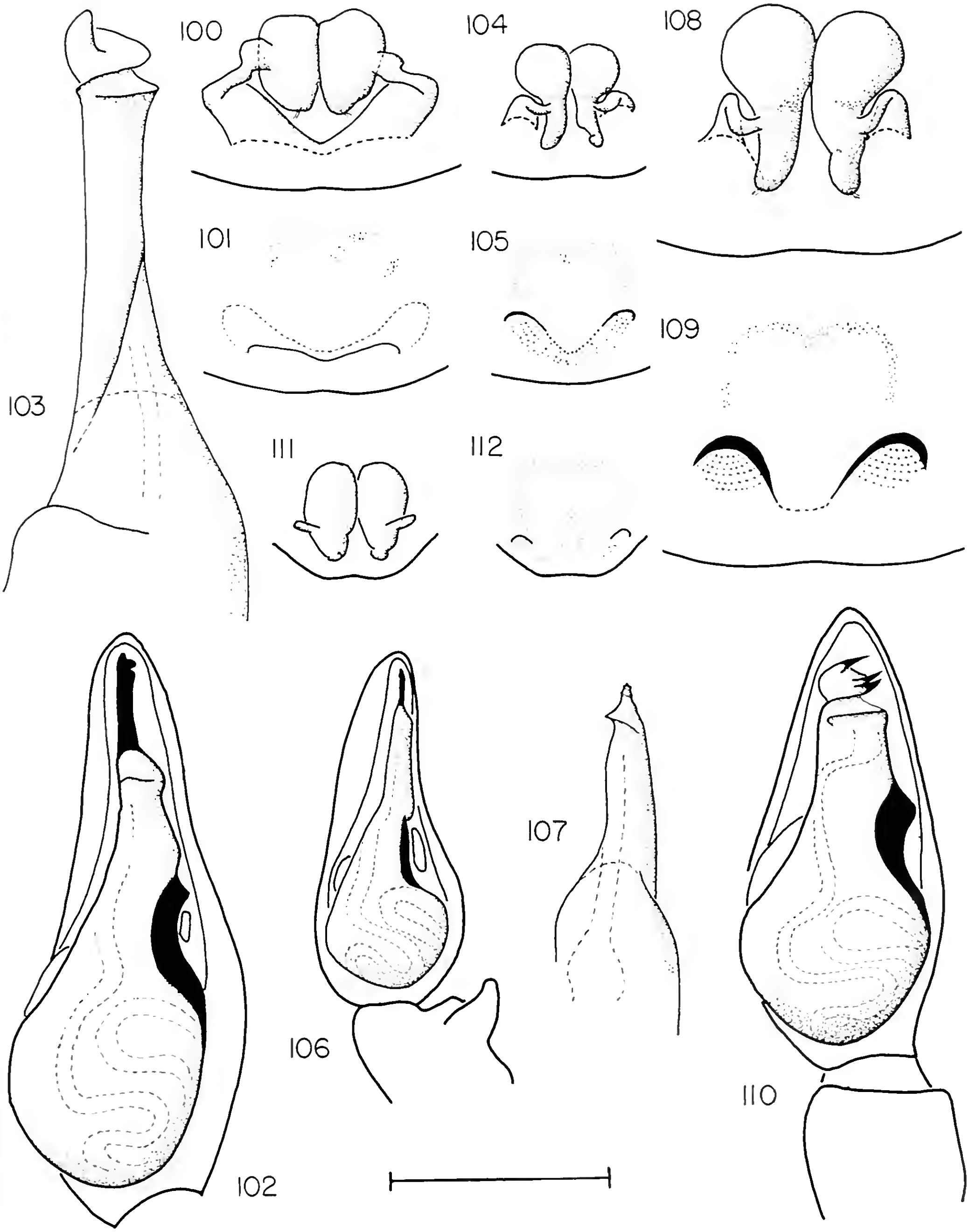
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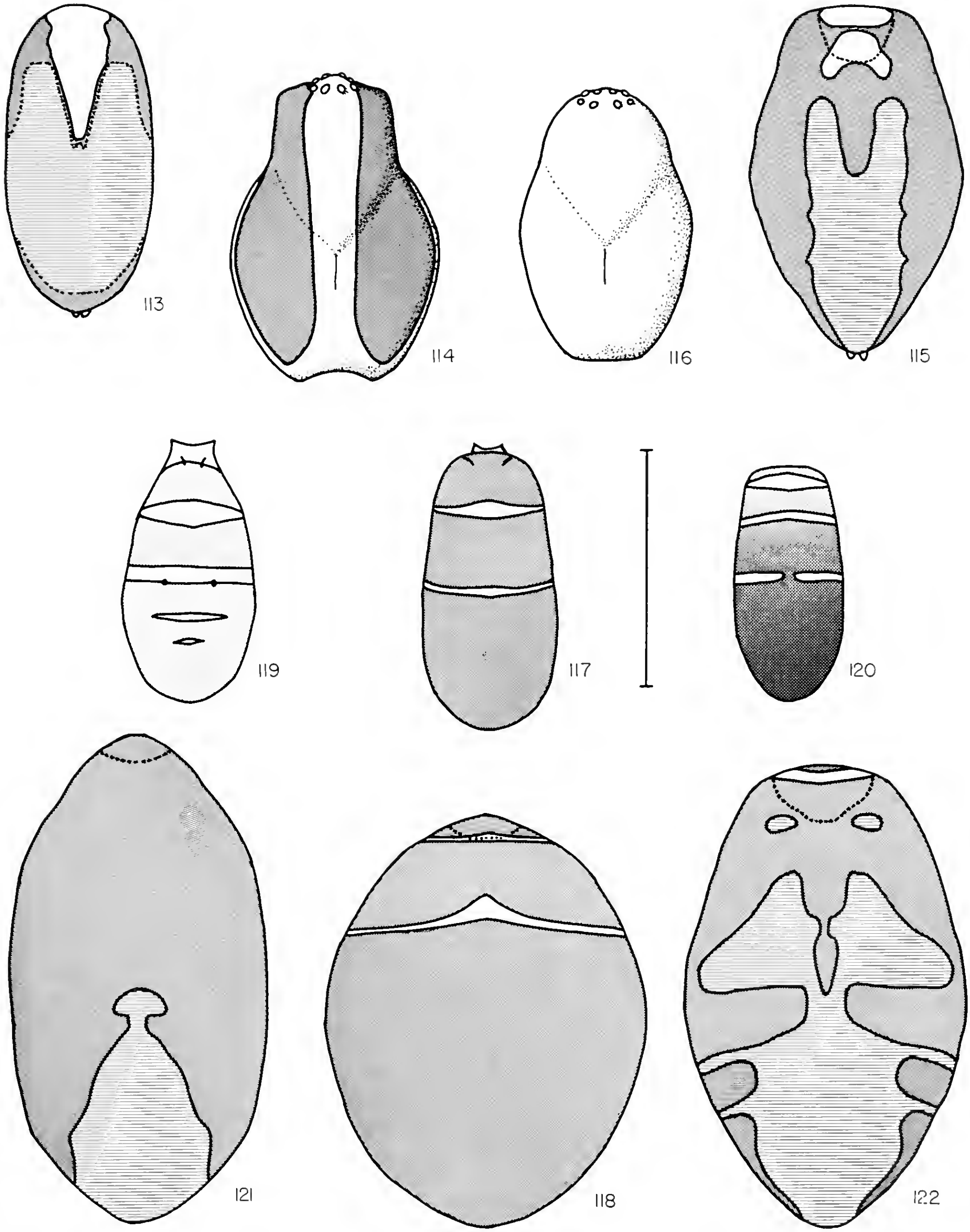
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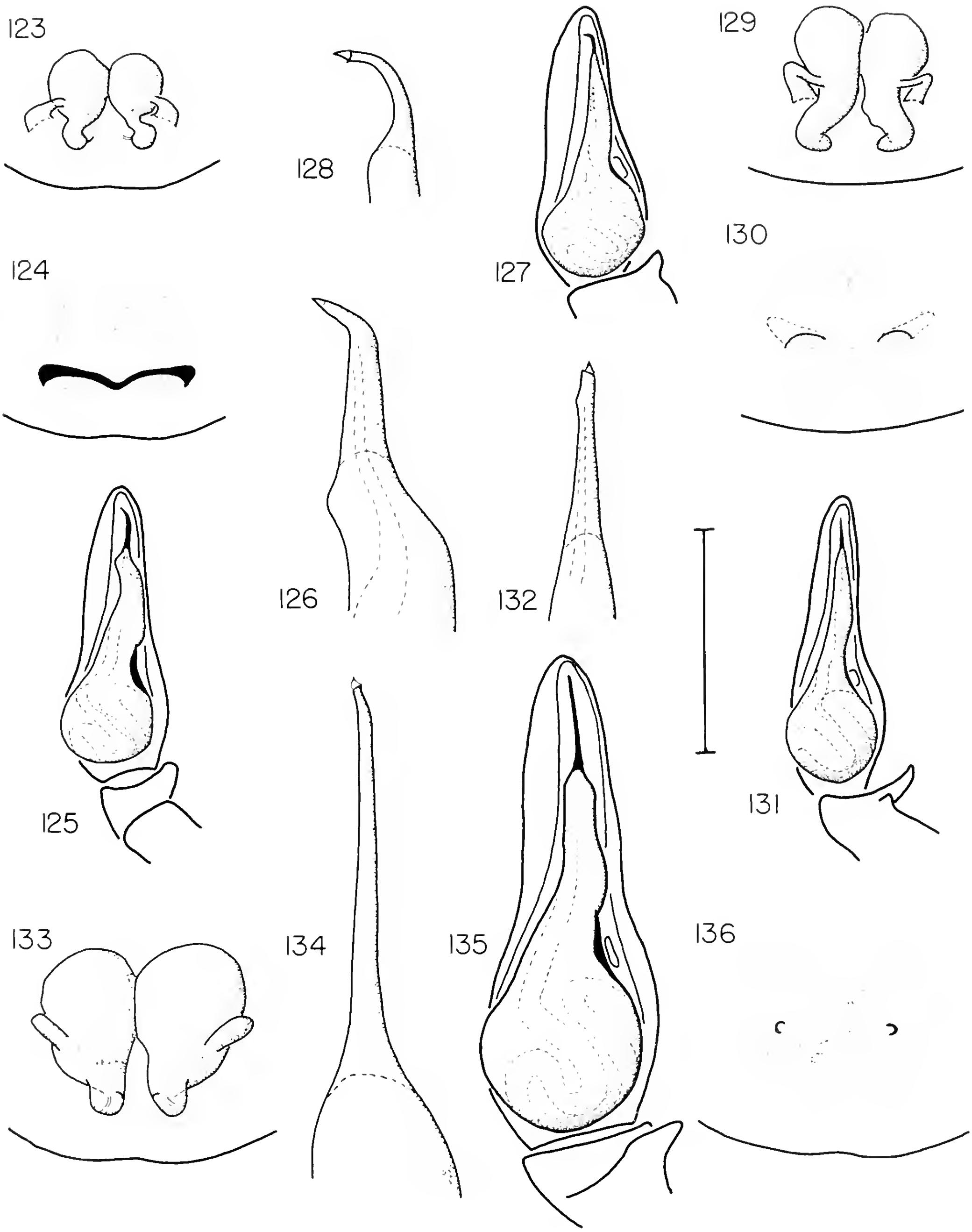
(Scale line for epigyna and palpi = 0.59 mm; for emboli = 0.15 mm.)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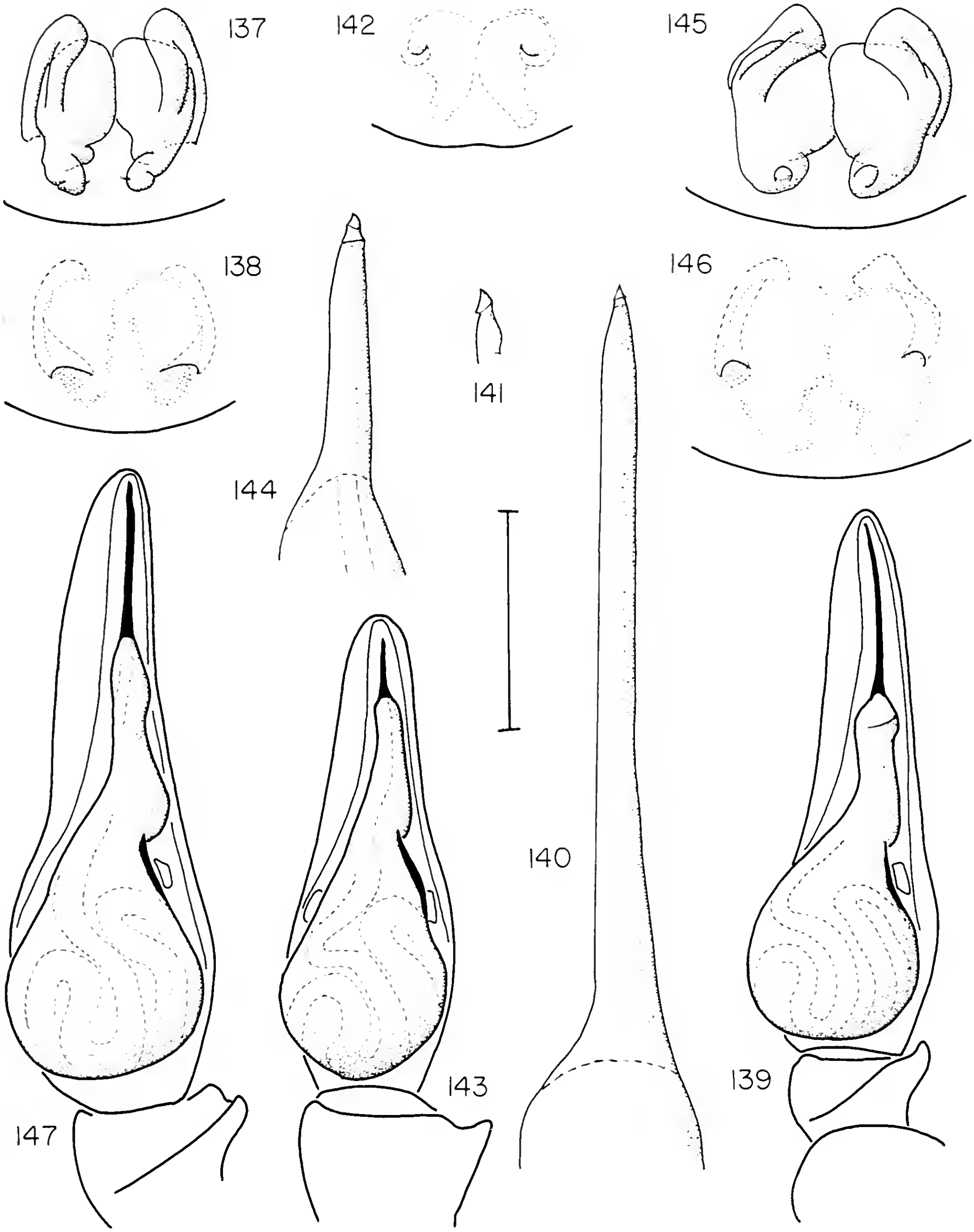
(Scale line for epigyna and palpi = 0.59 mm; for emboli = 0.15 mm.)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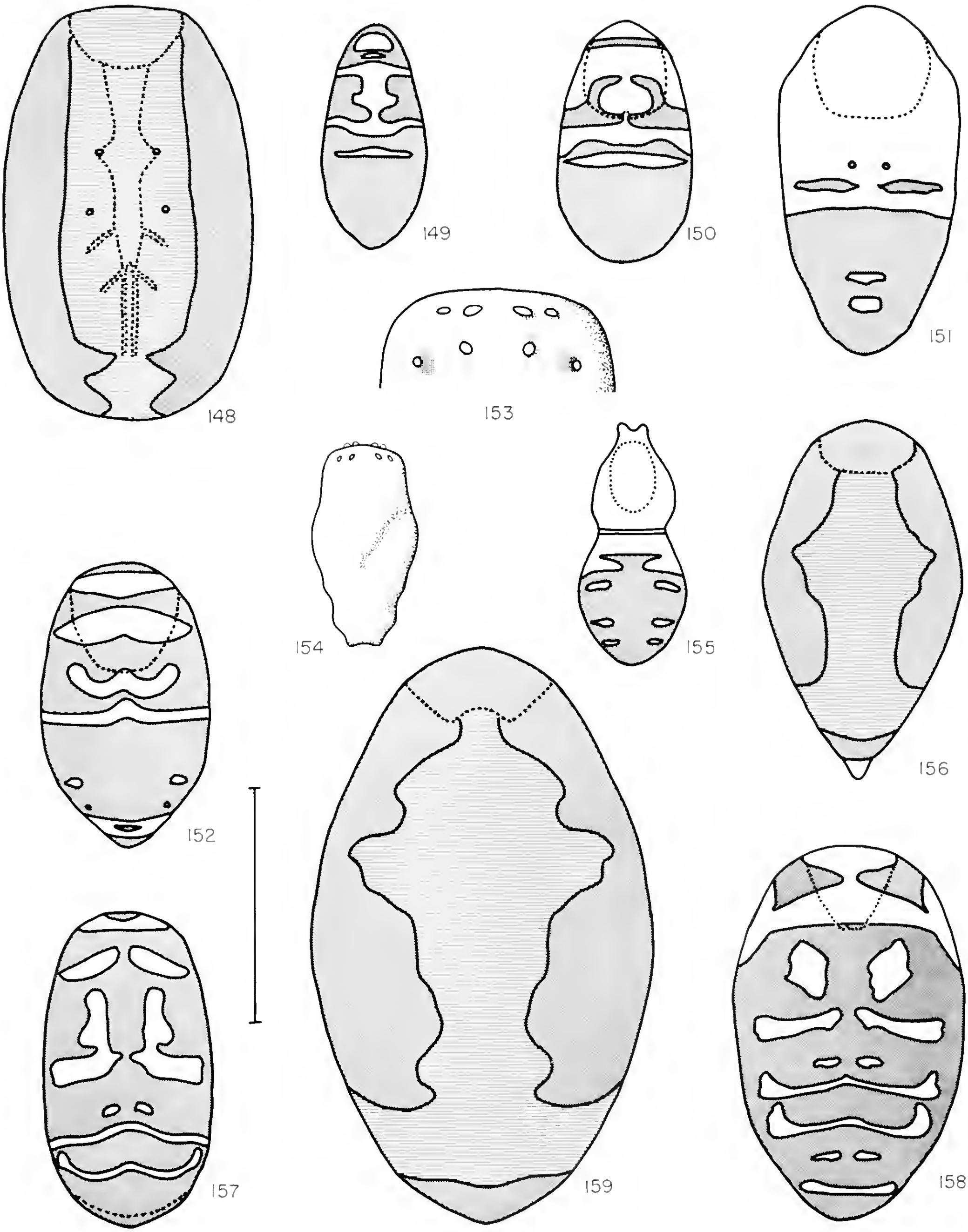
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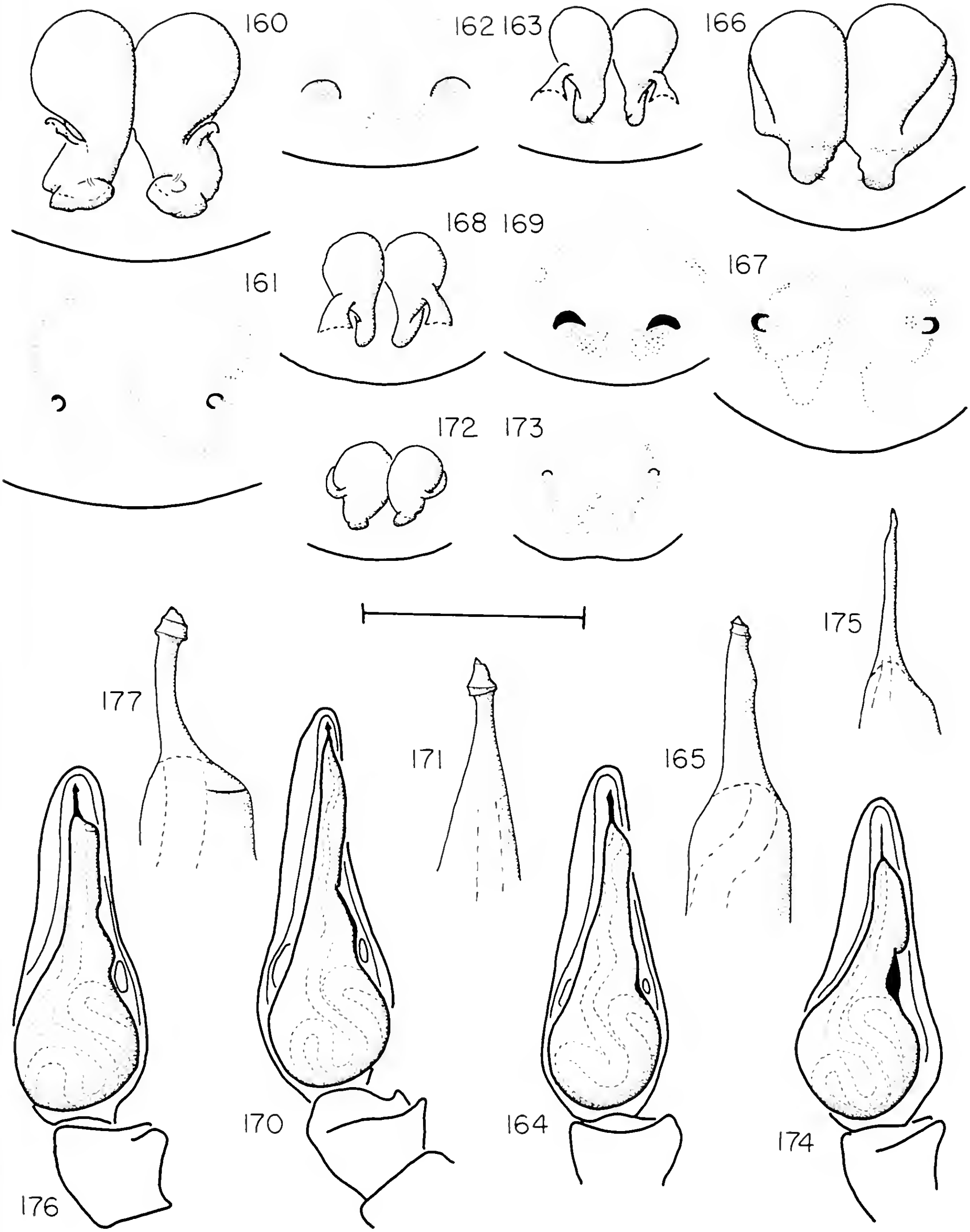
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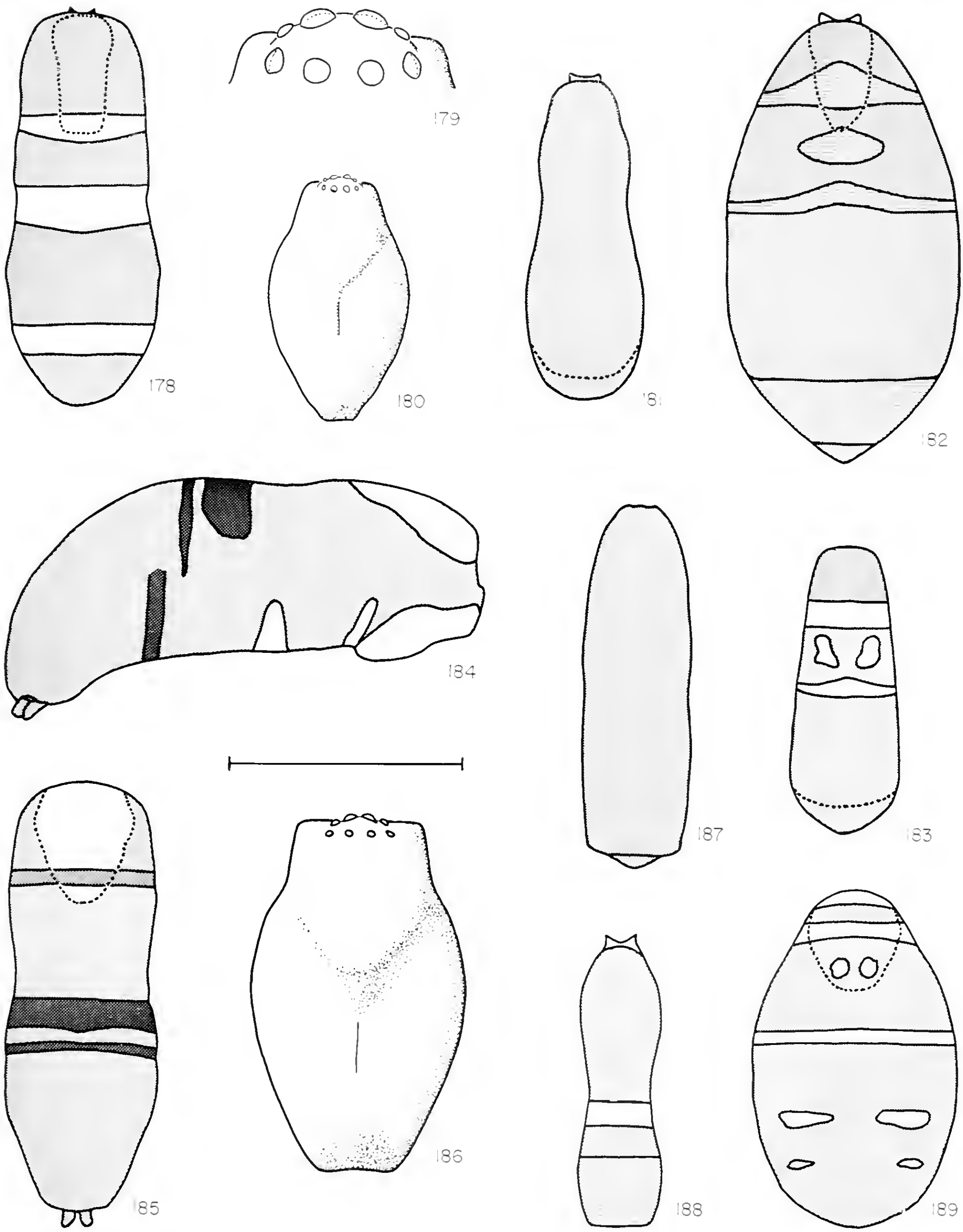
(Scale line for abdomens and carapaces = 2.72 mm; for eye region = 0.94 mm.)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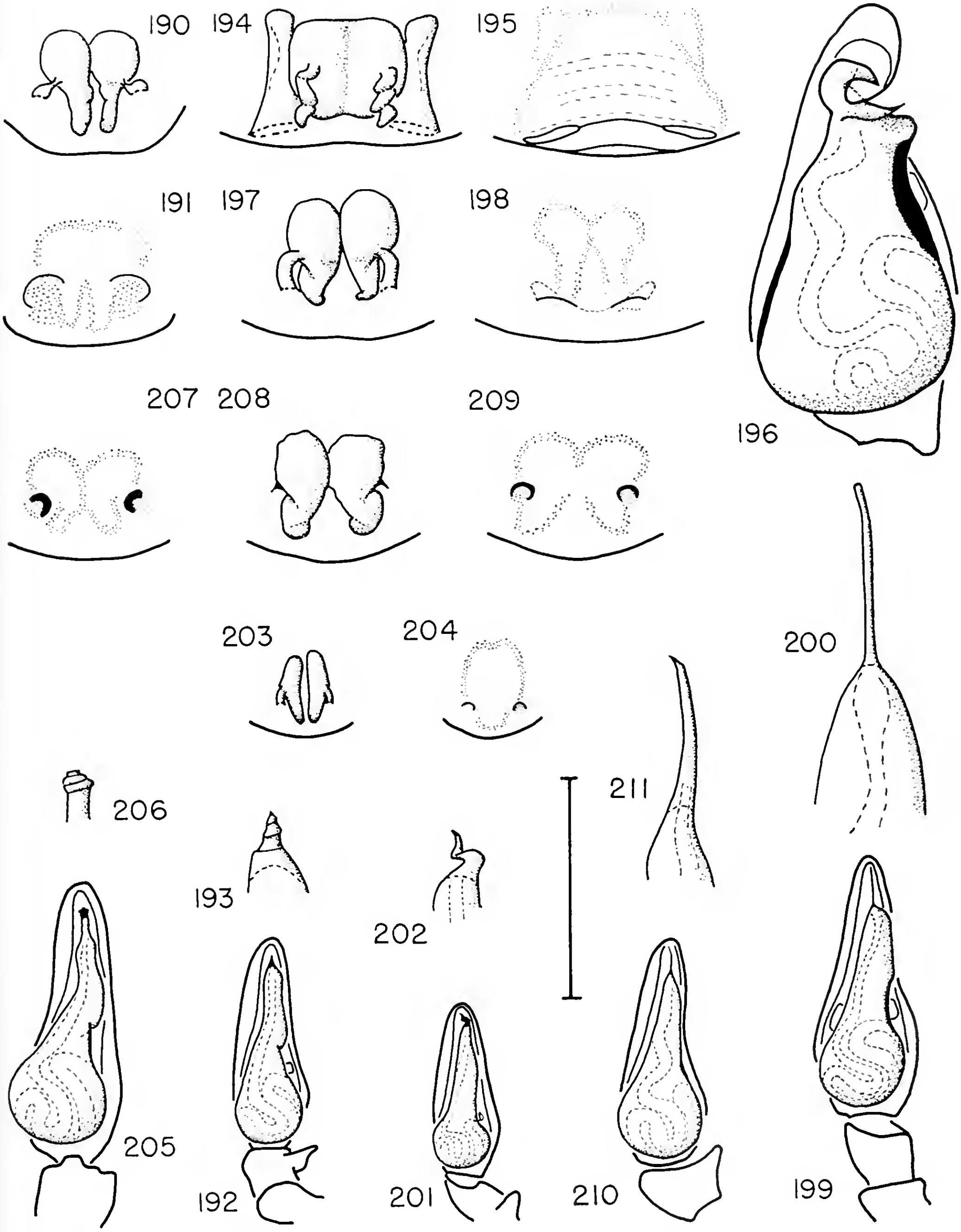
(Scale line for epigyna and palpi = 0.59 mm; for emboli = 0.15 mm.)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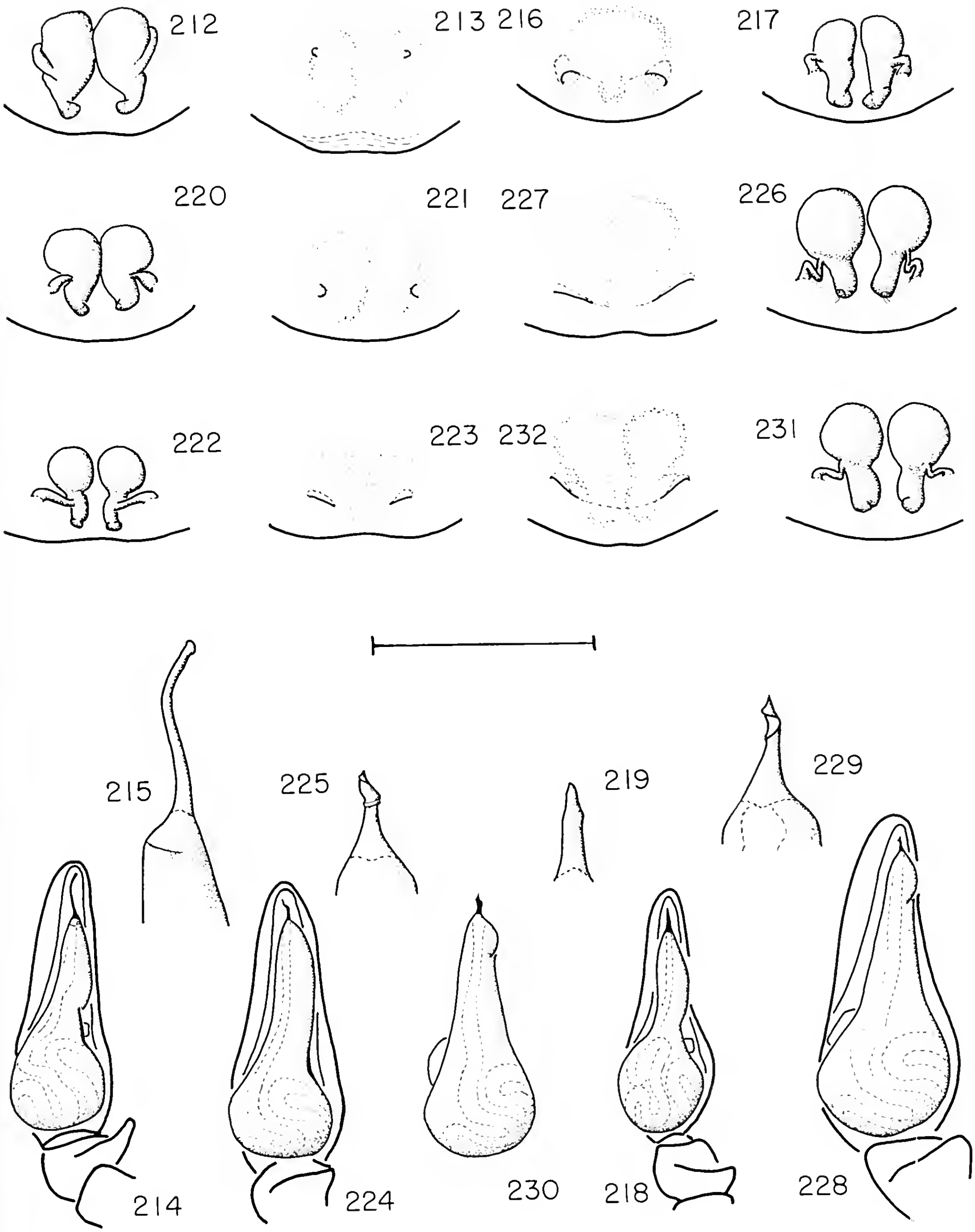
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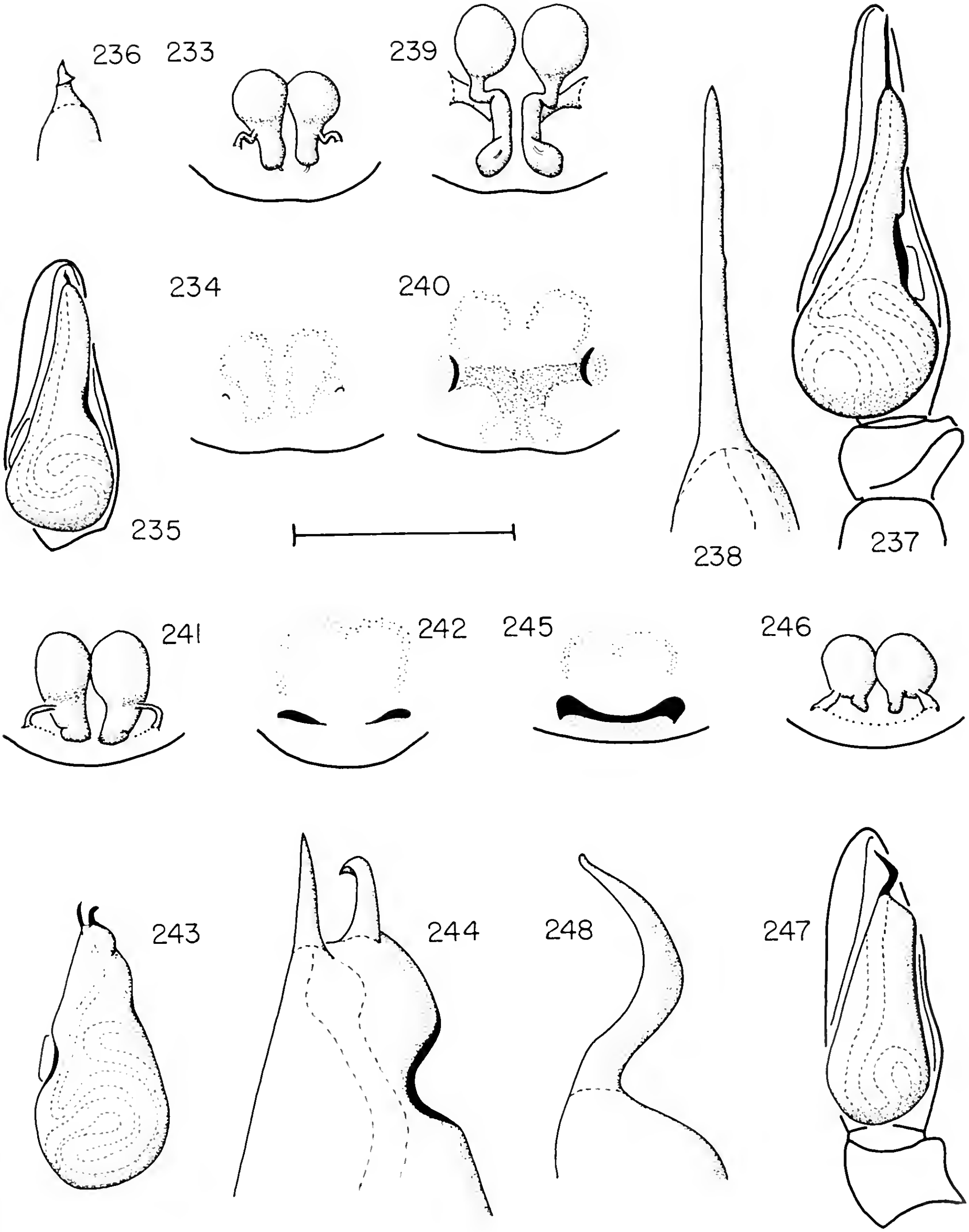
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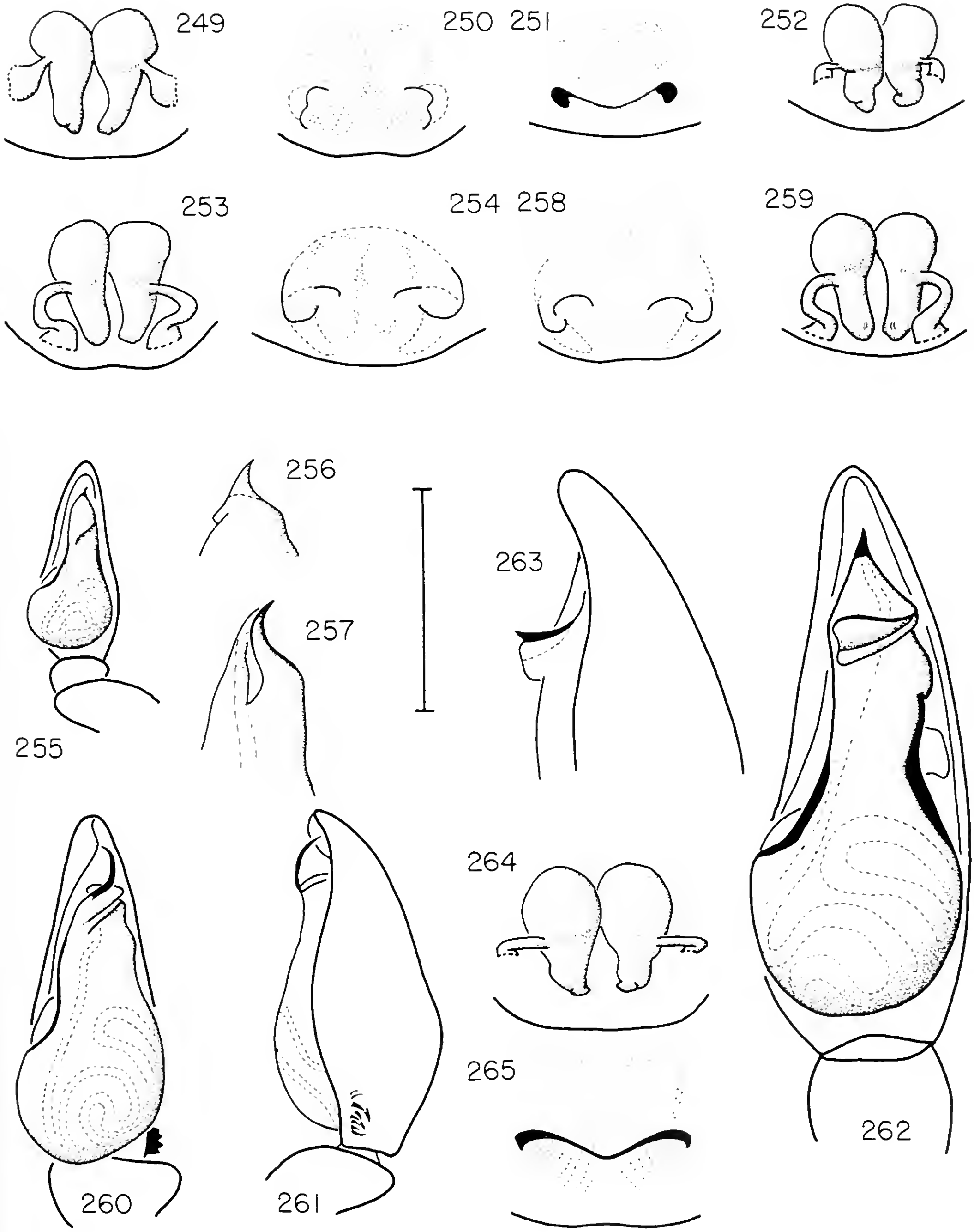
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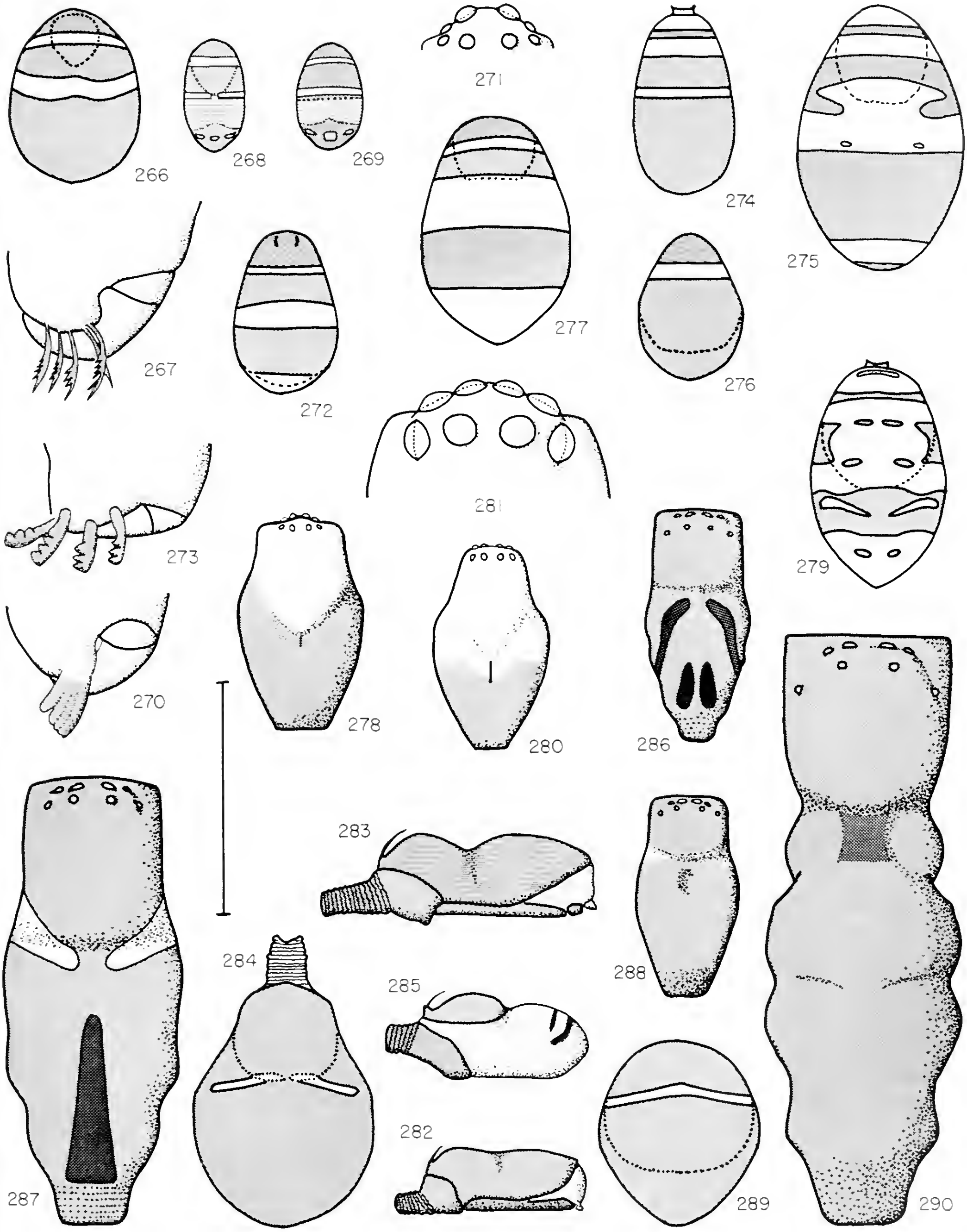
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Lizards and Snakes from Southwestern Asia, Collected by Henry Field

GEORG HAAS AND YEHUDAH L. WERNER

HARVARD UNIVERSITY
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LIZARDS AND SNAKES FROM SOUTHWESTERN ASIA, COLLECTED BY HENRY FIELD

GEORG HAAS[1] AND YEHUDAH L. WERNER[1]

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ABSTRACT

The squamate reptiles (428 specimens; 63 species and subspecies) collected by Dr. Henry Field in Syria, Iraq, Saudi Arabia, Iran, and West Pakistan (Peabody Museum–Harvard Expeditions, 1950 and 1955) are described. Each form is treated under the following headings: material examined (and localities), pholidosis, measurements, coloration, and remarks. Emphasis is put on the relatively abundant material of the genera *Agama, Acanthodactylus, Ophisops,* and *Eremias.* The meristic variation of large series is summarized in histograms and statistical tables. Two new forms are described: *Agama persica fieldi* and *Eremias brevirostris fieldi.* Several probable novelties are pointed out. The concluding discussion begins with a brief presentation (with map) of the two main views on the zoogeographical subdivision of Southwestern Asia: according to Bodenheimer, the Mediterranean Sub-region of Wallace is composed of three Sub-regions, Mediterranean, Irano-Turanian, and Saharo-Sindian, which together occupy a greater area than Wallace's Mediterranean. Regional species lists (of the above material) follow.

INTRODUCTION

The collection here reported on consists of 428 specimens of lacertilians, amphisbaenians, and ophidians, comprising at least 63 species and subspecies. It constitutes the squamate part of the herepetological material that was assembled by Dr. Henry Field during the Peabody Museum–Harvard University Expeditions of 1950 and 1955 (the amphibians and chelonians have not been examined by us). The material has been collected in Iraq, Iran, Syria, Saudi Arabia, the Persian Gulf (Bahrain Island and Trucial Oman Coast), and West Pakistan.

The huge area concerned (roughly 2400

[1] Attention is called to a paper by Loveridge (1959: 226–227) in which determinations are given for some specimens from West Pakistan (Baluchistan and Sind) and Saudi Arabia (Al Uqair).

km in W-E direction) presents strongly divergent landscapes, climates, and habitats, and its herpetofauna accordingly appears to be very diversified, few species (not to mention subspecies) ranging throughout the area. Indeed, the rich reptile fauna of Southwestern Asia is rather inadequately known. It is significant that since the publication of the second edition of the herpetological part of the Fauna of British India (Smith, 1931, 1935, 1943), a survey on herpetology has been compiled for only one of the five countries treated here (Iraq—Khalaf, 1959). Other relatively comprehensive recent papers, which we found particularly useful, are those on reptiles from Iran by S. C. Anderson (1963) and on the reptiles of West Pakistan by S. A. Minton (1966).

As will be seen, the present collection has two merits that greatly enhance its contribution to the knowledge of the herpetofauna of Southwestern Asia. First, many forms are represented by several specimens, or even by considerable series, from each of several localities. Second, much of the material originates from regions from which very few, if any, reptiles have hitherto been available. This applies in particular to the Luristan mountains in Iran and to the Makran hills of Baluchistan in West Pakistan (cf. Minton, 1966: 38).[1]

A number of presumably new subspecies, and perhaps species, are included in the collection, but in most cases we contented ourselves with merely pointing these out, since they should be treated by future revisers of the groups concerned in a more thorough manner than is feasible here. New forms are described here in only two instances, in which the material was particularly ample, distinct, and uniform: *Agama persica fieldi* and *Eremias brevirostris fieldi*. We are delighted to have had this opportunity to record both our recognition of Dr. Henry Field's continuous contribution, since 1927, to the advancement of the herpetology of Southwestern Asia and our own manifold indebtedness to him.

LOCALITIES

Figures 1, 2

All the localities at which material has been collected, in Syria, Iraq, and Iran, have been indicated on a tracing of a 1:4,000,000 map (Bartholomew, 1959, "The Middle East") by the collector, Dr. Field. These are represented as solid circles in Figure 1, whereas additional points of reference are represented as hollow circles. Localities in Saudi Arabia are given in Figure 2 (except Turaif, included in Fig. 1). Stations refer to Iraq Petroleum Company (IPC) Pipeline Stations.

List of Localities in West Pakistan

Big Kapoto, 10 mi. S of Kalat, Baluchistan
Quetta, Baluchistan
Nag, 75 mi. NE of Panjgur, Baluchistan
Little Kapoto, 10 mi. S of Kalat, Baluchistan
Pasni, Baluchistan
Saradoo, 28 mi. S of Panjgur, Baluchistan
Shahi-Tump near Turbat, Baluchistan
Shahi River, Kalat, Baluchistan
Zallaq, 5 mi. S of West Pakistan

Note. For locations see traverse maps in Field (1959).

METHODS

The techniques and procedures involved, although simple, are less standardized than is implied by the lack of explanations in most papers of this kind. The following statements may therefore be useful.

Regarding *taxonomic usage* we have followed, as far as feasible, the recommendations of Mayr, Linsley, and Usinger (1953). *Terms* are employed, as far as possible, in agreement with definitions cited in the Dictionary of Herpetology (J. A. Peters, 1964b).

Synonymy and references are given, under the heading for each species or subspecies, only to the extent required to justify and explain the name used.

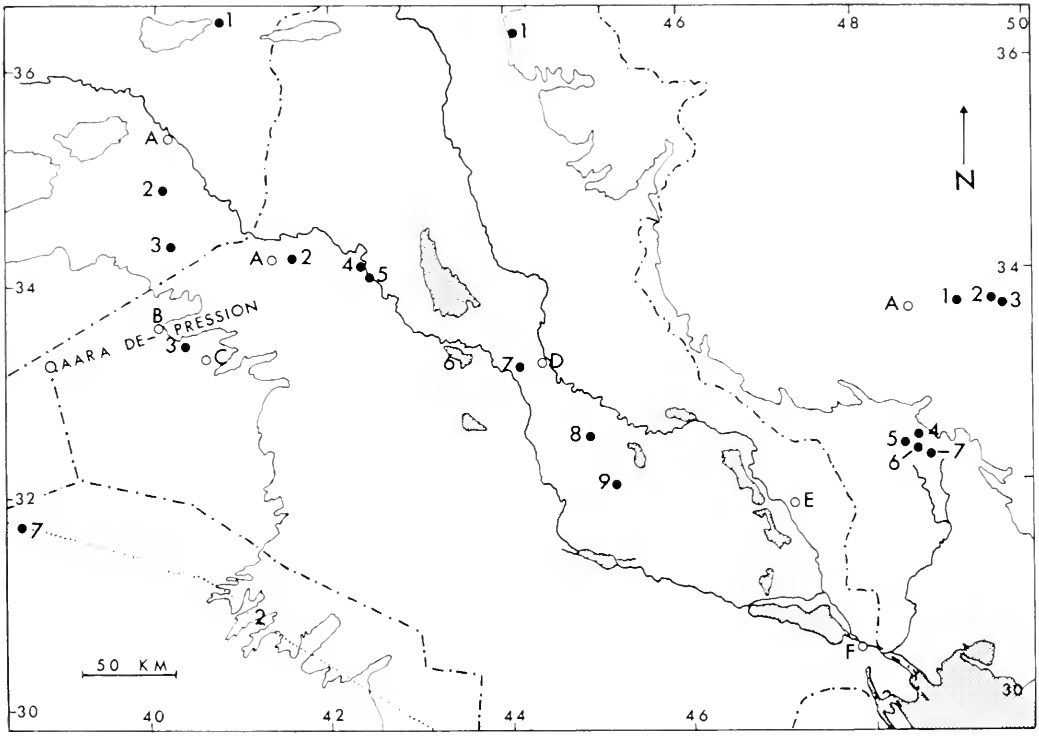


Figure 1. Sketch map of Iraq, western Iran, and adjacent territories. Collecting sites—solid circles. Other localities of interest or for reference—hollow circles. Key in text.

Key to Figure 1

SYRIA

1 Wadi Sukhura near Jebel Abdul Aziz, W of Hasseké (Hassetché)
2 20 mi. N of Station T-2
3 3 mi. NW of Station T-2
Qariatein-IPC Pipeline (excluded from map; ca. 50 km NE of Qariatein)
A Deir-ez-Zor

IRAQ

1 Havdian, at foot of Jebel Baradost near Ruwanduz (Rowandiz)
2 10 mi. E of Station T-1
3 Near Station H-2
4 Haditha, on the Euphrates
5 Station K-3 near Haditha
6 Lake Habbaniya
7 Abu Ghraib, W of Baghdad
8 Kish area, E of Hillah
9 Afaq (Afej)
Qaara Depression, N of Rutba
A Station T-1
B Bir Molusi (Meloza), N of Rutba
C Station H-2
D Baghdad
E Hor al-Hawiza, east of Amara
F Basra

IRAN

1 Zagheh
2 Dorud
3 Mazuo
4 Shalgahi
5 Dizful
6 Mahor Birinji
7 Gotwand
A Khurrumabad (Khorramabad)

SAUDI ARABIA

2 Trans-Arabian Pipeline (Tapline)
7 Turaif (ARAMCO Station VI) on Tapline

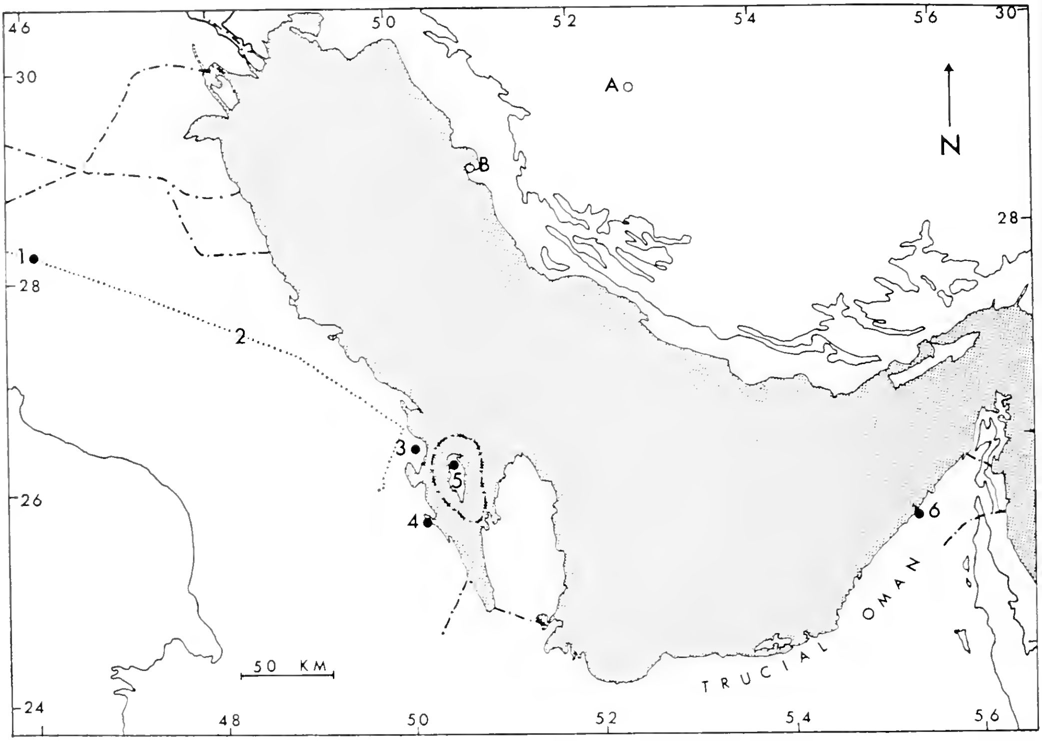


Figure 2. Sketch map of areas surrounding the Persian Gulf. Collecting sites—solid circles. Other localities of interest or for reference—hollow circles. Key in text.

Key to Figure 2

IRAN
- A Shiraz
- B Bushire

SAUDI ARABIA
- 1 Al-Gaisumah near Turaif on Tapline
- 2 Trans-Arabian Pipeline (Tapline)
- 3 Dhahran
- 4 Al Uqair

BAHRAIN ISLAND (No. 5)

TRUCIAL OMAN COAST
- 6 Sharjah

Conventional *scale counts* (depending on the genus concerned) were taken at least twice independently (see Acknowledgments), and if satisfactorily repeatable and deemed pertinent, are presented here. Where a series comprises up to five specimens, the individual figures for each character are given in the same order in which the respective specimens are listed under Material Examined. For larger series, the individual counts have, in most cases, been replaced by the following data of the sample: number of specimens (N), observed range (O.R.) of the character, its mean value (M), and its standard deviation (S.D.), based on the formula S.D.

$$\sqrt{\frac{\Sigma d^2}{N-1}}$$

(where d = deviation of any individual figure from the mean for that character). Thus anyone interested in the coefficient of variability or the standard error can derive these from our tables (Mayr *et al.*, 1953: 134, 141). The *ventrals of snakes* were counted beginning with the first scale

posterior to the gulars that is distinctly wider than long, and excluding the anal (Schmidt and Davis, 1941: 26).

Measurements of *snout-vent length* (= head and body) and of *tail length* were taken by pressing the specimen's ventral surface against a rigid, transparent millimeter ruler. Many of the snakes were strongly contorted, and then the measurements given are means between the results of this method and those obtained by applying a string along the midventral line of the body (which method usually gives too high a figure). All measurements of *head length* were taken parallel to the long axis of the body, by means of a metal ruler provided at its zero line with a broad stopper (against which the specimen's snout would abut) and along which an adjustable indicator could slide. In each case we specify in the text whether head length was taken to the occiput, to the posterior margin of the ear, etc. *Limbs* were measured from the axilla or the groin to the base of the most distal claw. Whenever possible, the limb was measured while it was stretched at a right angle to the body.

The *colors* of the specimens must have faded and changed considerably during the ten to fifteen years that passed between their preservation and our examination of them. Many specimens have obviously been darkened by overexposure to formalin. We therefore comment primarily on the pattern of the coloration, and mention colors only where apparently pertinent. In the circumstances, this is done in common sense terms, without reference to a color dictionary.

Our remarks certainly constitute no exhaustive discussion of each specimen or sample. We have only tried to hint at some of the main problems or (rarely) possible conclusions.

All line drawings were prepared by means of a camera lucida. The ruler included in the photographs shows cm and mm. In the photographs of dorsal scales we have superimposed on this ruler a scale bar representing 1 per cent of the snout-vent length of the respective specimen (at the same magnification). Thus the size of the scales can be interpreted without further reference to the size of the specimen.

The bibliography includes works both cited expressly in the text and consulted without citation.

SYSTEMATICS

ORDER LACERTILIA

Family Gekkonidae

Stenodactylus slevini Haas

Plate 1, A–C

Stenodactylus slevini Haas, 1957, Proc. Calif. Acad. Sci., (4) 29 (3): 54, fig. 3 (Dhahran, Saudi Arabia).

Material examined. SAUDI ARABIA (2): MCZ 56507–08, ♂♂, Saudi Arabia.

Pholidosis. The rostral has the typical middorsal depression and cleft. The strongly swollen nostril is surrounded by the rostral and three nasals, the first labial barely avoiding contact with the nostril. Upper labials: 12/12 and 15/15; lower labials: 14/13 and 13/13. Number of granules between superciliary ridges: at midorbital level, 32; 32; between the posterior corners of the eyes, 41; 49. No femoral or preanal pores. Each of the ventral granules, particularly posteriorly, culminates in a rosette of four or five "microtubercles" surrounding a central pit.

Measurements. Snout-vent: 52 mm; 54 mm. Tails missing. Diameter of eye (exposed portion): 4 mm.

Coloration. Rusty brown, including the ventral side; dorsal side with a close net of a delicate blackish reticulation. (Other preserved geckos in the same collection have retained a relatively lighter color on the ventral side.)

Remarks. The close similarity of these specimens to the original types is remarkable. The dark coloration of the ventral parts is very unusual, and may, after all,

TABLE 1. PHOLIDOSIS AND MEASUREMENTS OF *BUNOPUS BLANFORDII* AND *TUBERCULATUS*.

Locality and MCZ number	Upper labials	Lower labials	Tubercle rows on back[1]	Preanal and femoral pores	Lamellae under 4th toe	Snout to vent (mm)	Tail (mm)	Length of 4th toe from insertion of 5th (mm)
Arabia								
54407	12/13	9/9	16	0	24/24	47.0	22.0 + 16	8.5
54408	13/13	10/10	15	0	20/21	41.5	40.5 + 0	7.0
56516	10/12	10/11	15	0	24/23	49.0	48.0	7.0
Iraq								
56514	9/10	9/12	16	0	23/23	41.5	52.0	6.5
56515	10/10	9/10	15	10	23/22	40.5	50.5	7.0
Iran								
56509	9/10	8/9	15	2[2]	17/18	53.0	30.0 + 18	7.5
56510	10/9	10/9	15	0	18/24	34.0	39.0	5/5.5
56512	11/10	10/9	16	0	23/23	42.0	50.0	6.0

[1] Including lateral row, on each side, of small tubercles.
[2] Since our specimen has the usual caudal tubercles, it is not assignable to *B. biporus* F. Werner (1938: 267).

be an artifact. (It should be stated that the present specimens do not rank as metatypes, as we have not compared them to the types.)

Bunopus tuberculatus Blanford
Table 1

Bunopus tuberculatus Blanford, 1874, Ann. Mag. Nat. Hist., (4) 13: 454 ("in Gedrosia Persiaque," restricted by Smith [1935]: Baluchistan).

Material examined. SAUDI ARABIA (1): MCZ 56516, Saudi Arabia. IRAQ (2): MCZ 56514, 56515, Station K–3 near Haditha on the Euphrates. IRAN (3): MCZ 56509, 4 mi. W of Gotwand; MCZ 56510, 56512, Mahor Birinji.

Pholidosis. Nostril surrounded by the rostral, first labial, and three nasals. Meristic characters are detailed in Table 1.

Measurements. See Table 1.

Coloration. Rather more brownish than grey, and the dark crossbands much broader than in *B. blanfordii* (see below), their pigment not restricted to the tubercles. Tubercles between these bands share the general ground color and are not whitish as in *B. blanfordii.* The head pattern is disposed in a less orderly fashion than in *B. blanfordii*, but a dark lateral band through the eye is usually discernible.

Remarks. These animals look rather more heavily built than *B. blanfordii* from Arabia or from southern Israel (personal observation); in particular, the digits are thicker and shorter (see Table 1). The difference in the nature of the subdigital lamellae between the two species is considerable. (See also Remarks under *Cyrtodactylus scaber.*)

Bunopus blanfordii Strauch[1]
Table 1

Bunopus blanfordii Strauch, 1887, Mém. Acad. Sci. St. Pétersbourg, (7) 35 (2): 61, pl., figs. 13, 14 (Egypt [record believed to be erroneous, Schmidt, 1939: 55]).

Material examined. SAUDI ARABIA (2): MCZ 54407–08, ♀♀, Al Uqair, south of Dhahran, 15 February 1955, Dr. and Mrs. Henry Field.

Pholidosis. The nostril is surrounded by the rostral, first labial, and three nasals. The series of large preanal pores is continued nearly to the knee in MCZ 54408,

[1] Geckos of the genus *Bunopus* Blanford have been referred by Boulenger (1885, 1: 20) to *Alsophylax* Fitzinger. Leviton and S. C. Anderson (1963: 335–336) have reinstated *Bunopus* for those species that have dorsal tubercles, among which both *blanfordii* and *tuberculatus* are included.

and three-quarters of the way in MCZ 54407 (J. Anderson, 1896: 21). Meristic characters are given in Table 1.

Measurements. See Table 1.

Coloration. Dorsally light grey-beige; many of the tubercles, particularly on the flanks, are whitish, the others brown, producing a faint crossband pattern. The head (at least of MCZ 54407) with four pairs of incomplete, brown, longitudinal bands: first, from nostril to upper (anterior) corner of eye; second, through eye onto occiput; third, along upper labials through orbit and to ear; fourth, through lower labials, continued below ear. Tail with alternating brown and whitish half-rings. Ventral parts whitish, very finely mottled with light beige-grey. Regenerated portion of tail light brownish grey, almost uniform dorsally and ventrally.

Remarks. The digits of these two specimens are much more slender than those of *B. tuberculatus*, described above. The difference in actual length is expressed in Table 1. (See also Remarks under *Cyrtodactylus scaber.*)

Cyrtodactylus scaber (Heyden)

Stenodactylus scaber Heyden, 1827, *in* Rüppell, Atl. Reise Nördl. Afr., Rept., p. 15, pl. 4, fig. 2 ("Umgebung von Tor, Sinai"—Mertens, 1922).

Gymnodactylus scaber: Duméril and Bibron (in part), 1836, Erpétol. Gén., 3: 421.

Cyrtodactylus scaber: Underwood, 1954, Proc. Zool. Soc. London, 124 (3): 475.

Material examined. IRAQ (1): MCZ 56501, ♀, Afaq. IRAN (1): MCZ 56500, ♀, Shalgahi. TRUCIAL OMAN COAST (1): MCZ 56502, ♂, Sharjah.

Pholidosis. Internasal granules: 1; 1; 2. Upper Labials: 8/9; 9/11; 9/10. Lower labials: 9/9; 8/8; 8/8. Number of pairs of chin shields behind the postmentals (which meet): 1; 1/2; 1. Dorsal tubercles in 10 (±) longitudinal rows. The male has four preanal pores.

Measurements. Snout-vent: 32 mm; 30.5 mm; 35 mm. Only the second specimen has a complete tail: about 42 mm.

Coloration. Brownish grey. Back with three longitudinal series of darker brown blotches; the vertebral series continued onto the tail as dark half-rings. Ventral side somewhat lighter, excepting the distal quarter of the tail, which is as dark ventrally as dorsally.

Remarks. Specimens of *Cyrtodactylus scaber* are sometimes confused with *Bunopus,* because the classical distinguishing character—the angulated digits of the former—is easily misinterpreted. However, the appearance of *C. scaber* is really quite different from that of *Bunopus,* owing to the perfectly regular arrangement of the large dorsal tubercles in the former (but not in the latter). The presence of postmentals and chin shields in *C. scaber* (absent in *Bunopus*) constitutes a convenient criterion for conclusive differentiation.

Pristurus cf. *rupestris* Blanford
Plate 1, D

Pristurus rupestris Blanford, 1874, Ann. Mag. Nat. Hist., (4) 13: 454 (Muscat and Island of Karrack near Busheer [Bushire], Persian Gulf).

Material examined. PERSIAN GULF (5): MCZ 56517–21, Bahrain Island and Sharjah, Trucial Oman Coast.

Pholidosis. Internasal granules: 0–2 (1 in three specimens). Nostril surrounded by the rostral and three nasals. Upper labials: 5–7 (mean: 6.4). Lower labials: 3/4 – 5 (mean: 4.3). No dorsal ridge, nor tubercles on the flanks. Lamellae under 1st toe: probably 13 (starting point uncertain); under 4th toe: 23–25 (mean: 23.8).

Measurements. Snout-vent: 24.5–27 mm. All tails missing, broken at the base. Adpressed hindlimb reaches between shoulder and ear. Diameter of eye, about 1 1/4 mm (uncertain due to shrinkage); snout nearly 2.5 times as long.

Coloration. Two specimens have a light vertebral line and indications of five asymmetrical light transverse lines. The other

specimens are uniformly colored dorsally. All have the side of the head with a dark line through the round pupil, and the throat spotted with roundish blackish dots, each two to four granules in diameter. On the sides of the throat the spotted area extends backwards towards the axillae.

Remarks. The identification of this series remains doubtful because the number of labials is too low compared to Loveridge's data (1947: 73). The absence of tails presents a particular difficulty in the identification of *Pristurus* species. Our specimens do resemble *P. r. iranicus* Schmidt (1952: 2; 1955: 201–202) in the pattern of the throat and apparently in the length of the snout, which is longer than in typical *rupestris* (Smith, 1935: 64, fig. 20). The pholidotic characters, however, are not in agreement.

Phyllodactylus elisae (F.) Werner

Phyllodactylus elisae Werner, 1895, Verhandl. Zool.-Bot. Ges. Wien, 45; 14, pl. 3, fig. 1 a-e (Nineveh near Mosul, Iraq).

Material examined. IRAN (1): MCZ 56504, Mazuo.

Pholidosis. Upper labials: 12/13. Lower labials: 8/9. Dorsal tubercles: 14 in a diagonal row across the back.

Measurements. Snout-vent: 43 mm. Tail broken.

Coloration. Brown, tubercles and ventral side lighter.

Remarks. The presence of 14 rows of tubercles on the back is interesting; Werner's types had 10–12, and this seems to be the condition in Iraq generally (Khalaf, 1959), as we can confirm from two specimens (HUJ-R 1685) brought by Professor O. Theodor from Iraq in 1928. S. C. Anderson (1963), who reports on 18 specimens from Iran (collected not far from the locality of our specimens), makes no comment on this point.

Ptyodactylus hasselquistii ssp.

Lacerta hasselquistii Donndorff, 1789, Zool. Bytr., 3: 133 (Cairo, Egypt).

Ptyodactylus lobatus, Gray, 1825, Ann. Philos., (2) 10: 198.

Ptyodactylus hasselquistii: Duméril and Bibron, 1836, Erpétol. Gén., 3: 378, pl. 33, fig. 3.

Material examined. IRAQ (2): MCZ 56505–06, ♂♂, Station K-3 near Haditha on the Euphrates.

Pholidosis. The two specimens are nearly identical. The following data are given for comparison with Loveridge's table (1947: 279). Internasal granules: 1. Nasals surrounding nostril: 3 (nasal region elevated, nearly tubular). Upper labials: 12. Lower labials: 12; 10/11. Tubercle rows on back: 10 (tubercles small, conical, high). Scansors under 1st toe: 4(?), under 4th toe: 10/11; 10. (Lamellae under 1st toe 8+8, and under 4th toe 9+9.) Tubercle rows on tail: 1+1.

Measurements (the larger male). Snout-vent: 62 mm. Tail: 56 mm.

Coloration. Light brown with both lighter and darker spots. The light spots are whitish beige, somewhat roundish, and about 7–10 granules in diameter, excepting a series of vertebral blotches which are larger and less regular in shape and which continue onto the tail as light half-rings. The dark spots are blackish brown, larger than the light ones, and irregularly scattered among them, sometimes bordering on them; occasionally a dark spot surrounds a whitish one. Both types of spots combined cover roughly as much of the dorsal area as the ground color; from a distance, the animal looks mottled haphazardly in these three hues.

Remarks. Of the few specimens of this species recorded from Iraq, two from Haditha have been assigned by Schmidt (1939) to *P. h. hasselquistii.* Khalaf (1959) also says, "*P. hasselquistii hasselquistii* (Donndorff) is the probable subspecies in Iraq." However, the present specimens differ from those from Cairo (and southern Israel) in their less slender body proportions, shorter tail, and lower number of tubercle rows on the tail. It would not be prudent to base a new subspecies on these

two specimens; the more so since this species is well known for its high geographical variability (Flower, 1933; Y. L. Werner, 1965) and uncertain taxonomy (Loveridge, 1947; Wermuth, 1965). In general habitus and, especially, in coloration, our present two specimens resemble a series collected by Mr. Zinner at Sabkha, on the Euphrates, in northeast Syria.

Hemidactylus flaviviridis Rüppell

Hemidactylus flaviviridis Rüppell, 1835, Neue Wirbelth.-Fauna Abyss., Amph., p. 18, pl. 6, fig. 2 (Massawa Island, Eritrea).

Material examined. TRUCIAL OMAN COAST (1): MCZ 56503, ♀, Sharjah. WEST PAKISTAN (1): MCZ 54409, ♂, Shahi-Tump at Turbat, Baluchistan, 21 March 1955. Field.

Pholidosis. Upper labials: 15/16 (the 3 last very low); 12/12. Lower labials: 12/13; 8/10. No dorsal tubercles. Femoral pores: 0; 6/9. Lamellae under 4th toe: 13/14 (proximal ones tiny); 11/12.

Measurements. Snout-vent: 59 mm; 71 mm. Tails missing.

Coloration. On the grey-beige dorsum of MCZ 54409 there are five narrow, lighter, undulating crossbands. The dorsal skin on the other specimen is damaged.

Family Agamidae

Calotes versicolor (Daudin)

Agama versicolor Daudin, 1802, Nat. Hist. Rept., 3: 395, pl. 44 (India).

Calotes versicolor: Jerdon, 1853, J. Asiat. Soc. Bengal, 22: 470.

Material examined. WEST PAKISTAN (1): MCZ 54421, Nag, 4000 ft., 75 mi. NE of Panjgur, Baluchistan, 30 March 1955.

Measurements (half-grown). Snout-vent: 79 mm. Tail: 192 mm.

Coloration. Traces of seven dark crossbands on the body, and 28 dark rings on the tail, the first three to four incomplete ventrally, the last three to four confluent. Throat with about seven pairs of longitudinal (oblique) dark lines, partly continued onto the belly.

Agama agilis sspp.
(*Agama agilis agilis* Olivier)

Agama agilis Olivier, 1807, Voy. Emp. Othoman, 4: 394, pl. 29, fig. 2 (neighborhood of Baghdad).

Agama agilis agilis: Wettstein, 1951, Sitzungsber. Akad. Wiss. Wien, Math.-Naturw. Kl., Abt. 1, 160 (5): 433.

(*Agama agilis isolepis* Boulenger)

Agama isolepis Boulenger, 1885, Cat. Lizards Brit. Mus., 1: 342.

Agama agilis isolepis: Wettstein, 1951, Sitzungsber. Akad. Wiss. Wien, Math.-Naturw. Kl., Abt. 1, 160 (5): 434.

Material examined. IRAN (6): MCZ 56832–56837, Mahor Birinji. WEST PAKISTAN (8): MCZ 54413, Quetta, Baluchistan: MCZ 54414, Saradoo, 28 mi. S of Panjgur, Baluchistan, 24 March 1955; MCZ 54415, Shahi River, Kalat, Baluchistan, 21 March 1955; MCZ 54416–54420, Nag, 4000 ft., 75 mi. NE of Panjgur, Baluchistan, 30 March 1955.

Pholidosis. Scales around midbody: Iran, about 80–95; Pakistan, about 60–75, but 90 in MCZ 54414 (the single specimen from Saradoo). The taxonomy of this Rassenkreis appears to be more complicated than was assumed by Wettstein (1951). According to Wettstein, the Baluchistan population would belong to *isolepis* and the Iraq-North Iran populations to *agilis*. In our material, however, the specimens from Saudi Arabia (see later under *A. e. fieldi* n. ssp.) and from Iran conform to *isolepis* in the naris, which is clearly above the canthus rostralis (Boulenger, 1885). On the other hand, in most specimens from Pakistan the naris is just at or a trifle below the canthus (*A. agilis*, Boulenger, 1885). Only in MCZ 54420, a juvenile, is the naris clearly above the canthus and pointing directly upwards, not dorsocaudally as in the other specimens. Specimen 54420 is also remarkable for a rosette of six enlarged scales surrounding the pineal scale. Unlike those of the other specimens, its head scales are rather smooth and not convex, and its dorsal scales have

flat keels and are not mucronate. The spiny scales at the upper margin of the ear are fairly well developed in the specimens from Baluchistan. These spines are very short (not easily discernible) in the specimens from Iran.

The dorsal scales of the *isolepis*-like specimens from Iran show a rather abrupt change from the larger scales of the median area to the smaller lateral scales. This characteristic of *isolepis* has already been noted by Steindachner (1917: 14a). In all the specimens from Baluchistan this transition is very gradual. It is significant that Smith (1935) criticized Boulenger's (1885) separation of *isolepis* from *agilis;* whereas Boulenger (1890) regarded the specimens from India (and Baluchistan) as *isolepis*, Smith (1935) regarded them as *agilis*. Our materials from Baluchistan, by Boulenger's own criteria, fall mostly within *agilis*, only the one specimen 54420 being more *isolepis*-like.

Measurements. Largest from Iran (cf. *isolepis*)—Snout-vent: 94 mm. Tail 137 mm. Largest from West Pakistan (cf. *agilis*)—Snout-vent, 90 mm. Tail 167+ mm (incomplete; the next largest specimen, snout-vent 80 mm, has a tail of 148 mm).

Coloration. Iranian specimens (cf. *isolepis*)—Females have five dark dorsal crossbands between occiput and pelvis, each interrupted by five longitudinal light streaks. The dark half-rings of the tail likewise are interrupted by a light vertebral streak. The throat is adorned with about fifteen undulating dark longitudinal lines. Males are darker, with the dorsal pattern more diffuse and a blackish lateroventral zone; their throats are blackish medially, but laterally the female's pattern persists. A photograph of a male, female, and juvenile, with the same pattern as our specimens, has been published by S. C. Anderson (1963: 448, fig. 11).

West Pakistanian specimens (cf. *agilis*)—Dorsal pattern not discernible except for the light and dark half-rings on the tail. In the females, the throat is mottled with irregular dark and light longitudinal bands, the belly has a median straight dark band, and on either side about three undulating longitudinal bands. In the males, the throat and the ventrolateral areas are suffused with blackish, covering most of the aforementioned pattern. A photograph of a live male has recently been published by Minton (1966: pl. 17, fig. 2).

Remarks. The discussion by S. C. Anderson (1963: 444–451) should be consulted.

Agama cf. *persica* Blanford
Figure 3, B, C

Agama persica Blanford, 1881, Proc. Zool. Soc. London, 1881: 674, pl. 59 (Iran: Dehbid and Kázerun).

Material examined. IRAQ (1): MCZ 56857, ♂, Kish area, Hillah Liwa. SAUDI ARABIA (1): MCZ 56860, ♂, between Al-Gaisumah and Turaif.

Measurements. Iraq specimen—Snout-vent: 89 mm. Tail incomplete. Arabian specimen—Snout-vent: 118 mm. Tail: 181 mm.

Remarks. In pholidosis, both these specimens agree fairly well with Blanford's description, but there are certain discrepancies which preclude a conclusive determination. Thus, both have a laterally compressed tail, instead of a cylindrical one. The difference between the specimens is also disturbing: whereas the Saudi Arabian specimen has a straightly sloping forehead, that of the other is very convex and short. The Arabian specimen resembles Blanford's plate more closely than the other, yet the Iraq specimen shows traces of the (required) dark crossbands, whereas the Saudi Arabian animal is nearly uniform, occasional whitish tubercles excepted. Its tail has remnants of dark rings. The ventral coloration of neither agrees with Blanford's description: the Arabian specimen has a blackish throat and, along the belly, a grey median band and grey ventrolateral areas; the Iraq specimen has

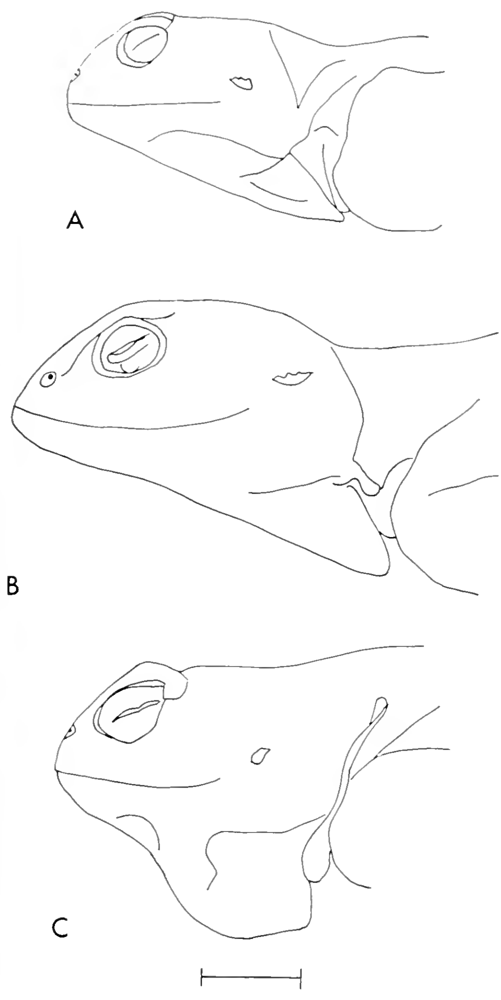


Figure 3. *Agama persica* sspp. Outline of head, lateral view, of:

A, *A. p. fieldi* subspec. nov., MCZ 56866, ♂ from Saudi Arabia (between Al-Gaisumah and Turaif).

B, *A.* cf. *persica*, MCZ 56860, ♂ from Saudi Arabia (between Al-Gaisumah and Turaif).

C, *A.* cf. *persica*, MCZ 56857, ♂ from Iraq (Kish area). All drawn to same scale. Scale bar: 10 mm.

three dark longitudinal bands along the whole trunk.

Apparently the taxonomic unit *persica* is a composite; a revision of this group of populations (possibly, of species), based on all available material, is desirable.

Agama persica fieldi subsp. nov.
Figure 3, A; Plates 2–6

(?)*Agama isolepis* Steindachner, 1917, Ann. k. k. Naturhist. Mus. Wien, 31: 147–149, pl. 3. (Mesopotamia: El Widian and Tekrit).

Holotype. Male, MCZ 56866, between Al-Gaisumah and Turaif, Saudi Arabia. Collected by Field in 1950.

Paratypes. Six: males, MCZ 56861–63 and 56867; females, MCZ 56864–65. Same locality and collector.

Other material. Two: male, MCZ 56859; female, 56858. Same locality and collector.

Diagnosis. Differs from *Agama persica persica* Blanford 1881 in having a conspicuous dorsal pattern of dark and light longitudinal bands and a distinct, though fainter, comparable ventral pattern; differs from *A. agilis* Olivier 1807 and *A. isolepis* Boulenger 1885 in the dorsal striped pattern and in that many specimens possess scattered enlarged dorsal scales.

Description of holotype. A male. Head longer than broad, with very convex forehead. Canthus rostralis continued as a superciliary ridge. Nostril on, barely above, the canthus, pierced in a flat shield. Upper head scales of two main types: anterior to the pineal spot, subimbricate, convex, some even pyramidal; posterior to the pineal spot, imbricate, keeled, and the most posterior mucronate. A double row of mucronate scales borders the ear from above and is continued to the end of the lateral surface of the head. Those of the lower row point downward, giving the ear opening an elongated appearance. Typical double gular pouch, the posterior fold extending onto the shoulder; but the pouch proper less deep than in typical *persica*. Body slightly depressed, head and body flatter than in other *persica*. Dorsal scales all strongly imbricate and distinctly keeled, otherwise variable. Four median rows are present. On each side there are two rows of larger scales that are distinctly mucronate, with upturned points. Further laterally the scales gradually diminish, those on the lower flank being smaller, having half the

length, or less, of the largest dorsolateral, mucronate scales. Ventral scales somewhat larger, rhomboidal, imbricate, and keeled. Among the scales on back and flanks there are occasional enlarged ones, about one and a half times as long as their neighbors. Altogether 76 scales around the middle of the trunk. Dorsal scales of limbs similar to middorsal scales; dorsal scales of tail similar to larger dorsolateral scales; all scales of these parts, excluding the smallest scales inside elbow and knee, are keeled. Limbs as in typical *persica;* tibia as long as head (to posterior border of ear). A single row of seven preanal pores. Scale rows of tail: 16 (counted between the proximal and middle thirds of the tail length).

Measurements of Holotype

	MM
Total length	245
Snout-vent	92
Head to occiput	17
Head to posterior border of ear	22
Head to jaw angle	25
Head width	20
Trunk length	75
Forelimb	42
Hindlimb	64
Tail	153

Coloration of holotype. A prominent pattern of longitudinal dark and light stripes. A light grey vertebral band of uneven width, with four constrictions between thorax and pelvis; this coincides with band of next-to-largest middorsal scales. On either side are three dark brownish bands, similarly of uneven width, with blackish margins, the ground color between them mottled with brown. Of the dark bands, the dorsal pair is the most conspicuous, the ventralmost pair the least so, merging with the flank's pattern. The latter is blackish brown, speckled with whitish spots, each of which occupies an enlarged scale. The dark bands are continued onto the head to the level of the posterior corner of the eye. Above the eyes, a pair of brown patches, and above the anterior corner of the eyes, an undulating crossband (shaped like an expanded M). On the tail, the pattern of bands gradually changes to one of blotches, followed by rings (on the distal half), each dark ring interrupted middorsally (except the few last ones). Similarly, brachium and femur with longitudinal bands, antebrachium and crus with transverse blotches. Throat with about 15 blackish lines, the lateral ones arranged on each side in three pairs, the medial ones confluent. Ground color of belly and ventral aspect of limbs a very light brown; belly with three darker grey longitudinal bands, the two lateral ones interrupted behind the axillae.

Variation of the type series. The range of the number of scale rows for the whole series (N=7) is 73–88, and the mean, 78.8. The four *male paratypes* resemble the holotype in all pertinent details. Scales around the middle of the trunk: 73; 80; 83; 77. No paratype is larger than the holotype. One male, MCZ 56862 has the dark throat pattern bluish black.

The two *female paratypes* have only traces of enlarged scales on back and flanks; these are the same color as their neighbors. Scale rows: 75; 88. The preanal pores are minute, each occupying the tip of a scale. The largest specimen measures 105 mm snout to vent, 167 mm tail (MCZ 56865). The throat pattern is best described as consisting of nine dark longitudinal bands, most of these being darker at their margins.

Range. Former material apparently assignable to the same form includes at least single specimens from El Widian and from south of Tekrit in Iraq (Steindachner, 1917), and one from Qa el Umari in northeastern Jordan (Y. L. Werner, in MS).

Remarks. This form is apparently allied both to *Agama persica* Blanford and to the *agilis-isolepis* complex. Since, presumably, specimens of the new forms collected in recent years have usually been referred to

persica, it seems most useful, at least for the time being, to regard the new form as a subspecies of the latter. This course is particularly justified by the close resemblance between the two in pholidosis and in the structure of the double gular fold; on the other hand, the subequal scales and somewhat depressed proportions argue for the relationship to *agilis-isolepis*.

Other material. The male and female entered under this heading above and collected on the same occasion as the type and paratypes are outstanding in having a mediodorsal stripe of very small scales, each slightly more than half the length of the neighboring dorsolateral scales. This median stripe of small scales extends from the occiput to the base of the tail. Furthermore, these two specimens have a paler coloration throughout, so that the belly has practically no pattern. The number of scale rows is within the range of *A. p. fieldi:* male, 74; female, 87. In the absence of further material, these two specimens may perhaps be regarded tentatively as an extreme form of *A. p. fieldi.*

Agama pallida Reuss

Agama pallida Reuss, 1833 (1834), Mus. Senckenb., 1: 38, pl. 3, fig. 3 (type locality in dispute—see Flower, 1933: 769).

Material examined. SYRIA (1): MCZ 56868, 10 mi. E of Station T-1. IRAQ (4): MCZ 56839, Haditha, on the Euphrates; MCZ 56840–56842, Station H-2. SAUDI ARABIA (14): MCZ 56843–56856, between Al-Gaisumah and Turaif.

Pholidosis. All these specimens have smooth ventrals (this comment is made because *Agama agnetae* Werner 1929, from Bir Meloza in Iraq, is distinguished by its keeled ventrals from *A. pallida* Reuss). In the specimens from Iraq and, especially, in the one from Syria, the small dorsals are keeled, as well as the large ones. In MCZ 56839, the dorsal tubercles form conspicuous transverse rows. In all specimens the ear is bordered above by three to four spines.

Measurements. Syria, a young male — Snout-vent: 57 mm. Tail: 71 mm. Iraq, largest male—Snout-vent: 76 mm. Tail: 96 mm. The largest female (containing eggs, obviously in the oviducts)—Snout-vent: 84 mm. Tail: 85 mm. The Arabian specimens are unusually large, with more slender proportions than those from Egypt, Sinai, or Israel. Largest male—Snout-vent: 93 mm. Tail: 127 mm. Largest female—Snout-vent: 91 mm. Tail: 106 mm.

Coloration. Syria and Iraq—The four dorsal transverse bands are inconspicuous, but usually the middorsal light interruption is discernible. On the tail there are about 12 dark crossbands. The throat is adorned with about 14 irregular dark grey lines. Saudi Arabia—The pattern is much less distinct, so that the dorsal crossbands are hardly discernible, and on the tail the crossbands (each uninterrupted, as in Iraq) are distinct only throughout the proximal two-thirds, or even half. The pattern of the throat is also more diffuse.

Remarks. All these specimens are quite different from those of eastern Egypt, Sinai, and southern Israel. The difference is even more marked when the material is taken as a whole, for in Israel males are much smaller than females. A study of this supposedly new form is at present under way (Y. L. Werner, in MS) on the basis of Jordanian material.

Agama melanura Blyth

Laudakia (*Plocederma*) *melanura* Blyth, 1854, J. Asiat. Soc. Bengal, 23: 738 (? Salt Range, Punjab).

Agama melanura: Boulenger, 1885, Cat. Lizards Brit. Mus., 1: 363.

Material examined. WEST PAKISTAN (1): MCZ 54412, Big Kapoto, 13 mi. S of Kalat, Baluchistan 4 April 1955.

Pholidosis. Dorsal scales are smooth. According to Smith (1935: 218), this is typical of specimens from the northern part of the range. The caudal scales are arranged in barely distinct annuli.

Measurements. Snout-vent: 121 mm. Tail: 207 mm.

Coloration. Black dorsally, and blackish grey ventrally. The tail is black ventrally, too, except for a light patch at its thick base. The lower sides of manus and pes are likewise relatively light colored.

Agama nupta nupta De Filippi

Agama nupta De Filippi, 1843, Giorn. Ist Lomb. Bib. Ital., 6: 407 (Persepolis).

Agama nupta nupta: Minton, 1966, Bull. Amer. Mus. Nat. Hist., 134 (2): 91–2.

Material examined. IRAN (1): MCZ 56838, Mahor Birinji.

Pholidosis. Enlarged dorsal scales in 16 rows.

Measurements (large female). Snout-vent: 144 mm. Tail: 215+ mm (tip missing).

Coloration. Dark Brown. Flanks mottled with roundish light brown spots. Almost all of the enlarged scales (middorsal and those on the limbs) are actually very dark brown with a lighter margin. The ventral parts are light brown; throat irregularly mottled with black; abdomen and hindlimbs rather yellowish.

Agama caucasica ssp.

Stellio caucasicus Eichwald, 1831, Zool. Spec., 3: 187 (Tiflis and Baku, Caucasus).

Agama caucasica Boulenger, 1885, Cat. Lizards Brit. Mus., 1: 367.

Material examined. WEST PAKISTAN (1): MCZ 54411, Little Kapoto, 10 mi. S of Kalat, Baluchistan, 4 April 1955.

Pholidosis. About 175 scales around midbody (against 150–160 according to Boulenger). A narrow middorsal band of enlarged, weakly mucronate scales, six scales broad. On either side a dorsolateral band, about 50 scales broad, of tiny scales. On the flank 10 rows of very spiny scales. Groups of spines, especially in the cervical region. Our specimen is a male; the ventral patch of "pores" is about 23 scales long, about 8 wide. Two to three irregular preanal rows.

Measurements. Snout-vent: 134 mm. Tail (incomplete): 154 mm.

Coloration. Very dark. The throat is spotted with distinct lighter spots: several small roundish ones anteriorly, and three large, longitudinal ones posteriorly.

Remarks. Although this single specimen agrees in certain respects with Guibé's (1957) *A. c. mucronata* from Iran, it differs from the latter in that, amongst other things, its tympanum is not wider than the eye, and there are no spines around the tympanum.

Phrynocephalus scutellatus (Olivier)

Agama scutellata Olivier, 1807, Voy. Emp. Othoman., 3: 110; 5: 196; Atlas, pl. 42, fig. 1 (near Isphahan, now Isfahan, Persia).

Phrynocephalus olivieri Duméril and Bibron, 1837, Erpétol. Gén., 4: 517.

Phrynocephalus scutellatus: Smith, 1935, Fauna Brit. India, Rept. Amph., 2: 229.

Material examined. WEST PAKISTAN (24): MCZ 54422–29 and 12 unnumbered specimens, Nag, 4000 ft., 75 mi. from Panjgur, Baluchistan, 30 March 1955; MCZ 54430–33, Saradoo, 28 mi. S of Panjgur, Baluchistan, 27 March 1955.

Pholidosis (of the numbered specimens). Scales around midbody 111–153 (±5); mean, 128 (N=12). Of these, scales across the belly, 40–45. Dorsal scales subequal; there are no real enlarged nail-like scales among them, as described by Smith (1935: 229), but such scales are also not mentioned by Minton (1966: 97), who deals with Pakistanian specimens.

Measurements. Largest male (MCZ 54422)—Snout-vent: 49 mm. Tail: 69 mm. Largest female (MCZ 54430)—Snout-vent: 44 mm. Tail: 58 mm. Fore- and hindlimbs of males reach, adpressed, beyond the snout.

Coloration. The dark crossbands on the back are discernible in few specimens; apparently there are three to five. On the base of the tail there are one or two dark crossbands, behind these five or six dark annuli. These are darker, almost black, ventrally, contrasting with the cream-white

ventral ground color. The tip of the tail is whitish ventrally, grey dorsally, for a length about equal to the head length.

Remarks. The maximum size given here is greater than that given by Minton for specimens from West Pakistan (1966: 97—males, 44 mm snout-vent; females, 46 mm).

Phrynocepahlus cf. *maculatus* J. Anderson

Phrynocephalus maculatus J. Anderson, 1872, Proc. Zool. Soc. London, 1872: 389 (Awada, Shiraz, Persia).

Material examined. TRUCIAL OMAN COAST (1): MCZ 56969, Sharjah.

Pholidosis. The nostril is invisible from the dorsal aspect, directed upwards and forwards. Nasals separated by three series of scales. There is no lobe at the angle of the mouth. Dorsal scales homogeneous.

Measurements. Snout-vent, 66 mm. Tail: 90 mm. Adpressed hindlimb reaches eye.

Coloration. Dorsum brown, speckled yellowish, with indications of darker crossbands (?4), which are interrupted middorsally. Tail with dark crossbands, every second of which is broader and better defined. Tip blackish. A photograph of a live specimen showing the same pattern is given by Minton (1966: pl. 18, fig. 3).

Remarks. The specimen certainly is assignable to neither *P. arabicus* nor *P. nejdensis*.

Uromastix microlepis Blanford
Plate 7

Uromastix microlepis Blanford, 1874, Proc. Zool. Soc. London, 1874: 656, pl. 53 (Basra, Iraq).

Material examined. SAUDI ARABIA (2): MCZ 56830–31, between Al-Gaisumah and Turaif.

Measurements (juveniles). Snout-vent: 110 mm; 107 mm. Tail of the first: 77 mm (the second lacks the tip).

Coloration. Evidently juvenile coloration. Dorsum blackish brown with about six somewhat irregular yellowish crossbands; these are interrupted dorsolaterally so that each consists of one to two vertebral spots and lateral bands. Below the eye there are three light vertical bars. Underparts a pinkish light brown, throat speckled heavily with grey-brown.

Uromastix loricatus Blanford

Centrotrachelis loricatus Blanford, 1874, Proc. Zool. Soc. London, 1874: 660 (Bushire, Iran).
Uromastix loricatus: Boulenger, 1885, Cat. Lizards Brit. Mus., 1: 409, pl. 32.

Material examined. IRAN (1): MCZ 56829, 15 mi. S of Shalgahi.

Measurements. Snout-vent: about 22 cm. Tail: about 16.5 cm. (The specimen is badly contorted.)

Coloration. Dorsum brown, with some of the tubercles yellowish. On the tail, some groups of contiguous tubercles yellowish. Ventrally, light yellowish brown; but throat, forelimbs, and femur the same brown as dorsally. Two brown crossbands in pectoral region.

Family Lacertidae

Lacerta trilineata media (Lantz and Cyrén)
Figure 4, A, B

Lacerta viridis media Lantz and Cyrén, 1920, Bull. Soc. Zool. France, 45: 33 (Tiflis, now Tbilisi, Transcaucasia—Mertens and L. Müller, 1940).
Lacerta trilineata media: L. Müller, 1939, Izv. tsarsk. prirodnauch. Inst. Sofia, 13: 12.

Material examined. IRAQ (6): MCZ 56665, ♂, 56667–71, juveniles, Havdian, at foot of Jebel Baradost near Ruwanduz.

Pholidosis. All specimens have four pairs of large submaxillary shields. Superciliary granules: 7–9 (11 on one side of the adult); mean, 8.3; S. D., 1.21. All specimens have two postnasals and a single anterior loreal on each side. Scales across middle of back: 48–55; mean, 51.5; S. D., 3.02. Longitudinal series of ventral plates: 6 (the enlarged series of marginals counted among the dorsals). Plates in collar: 7–11; mean, 8.8; S. D., 0.42. Gular scales in straight median series: 18–23; mean, 21; S. D., 1.90. Femoral pores: 11–14; mean, 12.7; S. D., 1.03. Subdigital lamellae (4th toe): 26–28; mean, 27.3; S. D., 0.82.

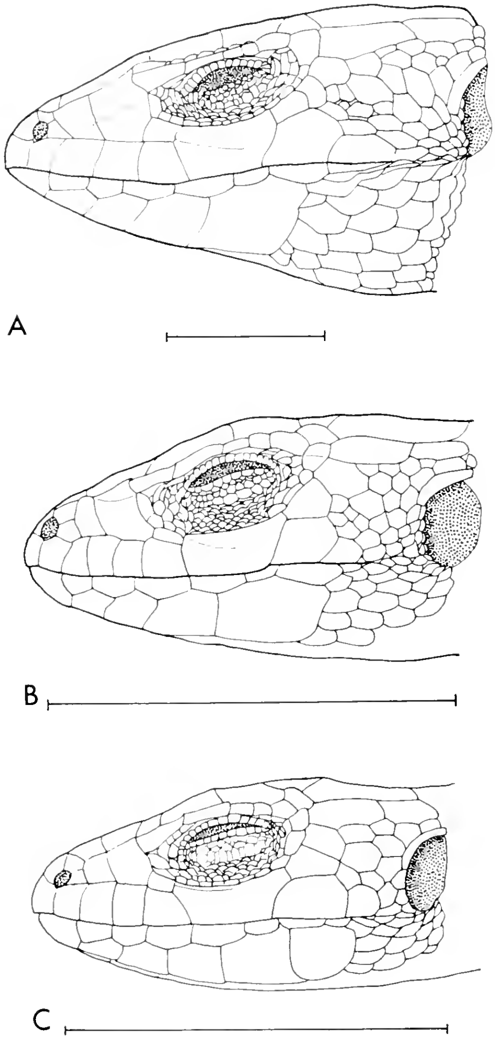


Figure 4. *Lacerta* spp. from northern Iraq. Head, lateral view, of:
A, *L. trilineata media*, MCZ 56665, adult ♂.
B, *L. t. media*, MCZ 56671, juvenile.
C, *L.* cf. *strigata*, MCZ 56666, juvenile (?). Scale bars: 10 mm.

Measurements. The adult male—Snout-vent: 128 mm. Tail: 260 mm. The juveniles—Snout-vent: 36–44 mm. Tail: (n=2): 177–190 per cent of snout-vent length.

Coloration. The adult male shows scarcely any distinguishable pattern. The whole head is covered with a fine blackish reticulum of vermiform lines; the dorsal scales of the tail and the larger scales of the limbs are similarly adorned. Most ventral scales (of all parts) are a dark grey with light margins. All juveniles have a light vertebral line from occiput to pelvis; on either side there are two similar lines, and a third interrupted one. The five medial lines are sharply delimited, each about two scales broad; the lateralmost pair coincides with the marginalia.

Remarks. The pholidosis of our material is in perfect accord with the diagnosis given for this subspecies by G. Peters (1946a: 243). It is interesting to compare the mean values of our counts with those mapped by Peters (1964a: figs. 2–8). While most of our values are more or less the same as those found in the areas of Adana-Amanus and Armenia, or intermediate between them when these differ, the number of scales across the back is somewhat higher in Havdian. The difference in tail length between our male (203% of snout-vent length) and juveniles (177–190%) is in full agreement with the ontogenetic allometry described by Peters (1964a: fig. 10).

No *Lacerta trilineata* has apparently been recorded from Iraq so far (nor, indeed, any member of the genus *Lacerta*). The range of *L. t. media* covers, according to Mertens and Wermuth (1960: 150), northeast Asia Minor, the Caucasus, and the areas to the southeast, to Mardin (SE Anatolia). Peters (1964a: 243) gives a broader range, including part of Iran, to the neighborhood of Isfahan (Isphahan) (map, Peters, 1962: fig. 4).

Lacerta cf. *strigata* Eichwald
Figure 4, C

Lacerta strigata Eichwald, 1831, Zool. Spec. Ross. Pol., 3: 189 (Krasnovodsk, North Caucasus).

Material examined. IRAQ (1): MCZ 56666, juvenile, Havdian, at foot of Jebel Baradost, near Ruwanduz.

Pholidosis. Five pairs of large submaxillary shields, the fifth slightly larger

than the second. Superciliary granules, 2/3. Nostril bordered by the rostral, first labial, one anterior and two posterior nasals. One anterior loreal. Scales across middle of back, 36. Longitudinal series of ventral plates, eight (marginalia excluded). Plates in collar, nine (the five median ones largest; outermost pair very small). Gular scales in straight median series, 14. Femoral pores, 17/?. Lamellae under 4th toe, 27.

Measurements. Snout-vent, 38.5 mm. Tail: 80 mm (208% of snout-vent length). Head (to rear border of ear): 11.5 mm. Foot: 12.5 mm.

Coloration. Dorsally, no discernible pattern. Ventrally, most scales dark with a lighter margin.

Remarks. This lizard was collected at the same locality as the series of *Lacerta trilineata media* reported here, but differs markedly from all specimens (juveniles) of that series in pattern and proportions, and (from the adult, as well) in pholidosis. The single, apparently juvenile, colorless specimen cannot be identified with certainty. The participation of the rostral in the nostril, the large temporal scales, the large 5th pair of submaxillary plates, and the foot, which is approximately as long (in relation to the head) as in the young *L. t. media,* all argue for relationship with *L. strigata.* However, Peters (1962: 135) does not know of any *L. strigata* with eight rows of ventral plates, and juvenile *L. strigata* always have a striped pattern. Thus our specimens appear to be related to, but not identical with, *L. strigata* Eichwald. (We may add that this specimen is certainly not similar to *Lacerta agilis brevicaudata* from Armenia, judging from its description by G. Peters [1958].) Furthermore, *L. strigata* is so far known to be sympatric with *L. t. media* only near the northeastern border of the latter's range (between Lake Urmia [Rizaiyeh] and the Caspian), while the locality of our dubious specimen (between Lake Urmia and the Tigris River) coincides with the southwestern frontier of *L. t. media* (in Iran; map, Peters, 1962: fig. 4).

Acanthodactylus boskianus asper (Audouin) Plate 8, D

Lacerta aspera Audouin, 1829, Descr. Egypte, Rept., Suppl., p. 173, pl. 1, fig. 9 (Egypt).
Acanthodactylus boskianus var. *asper:* Lataste, 1885, Ann. Mus. Civ. Stor. Nat., Genova, (2) 2 (22): 496.

Material examined. IRAQ (1): MCZ 56642, ♂, Station K-3 near Haditha. SAUDI ARABIA (1): MCZ 56643, ♂, between Al-Gaisumah and Turaif.

Pholidosis. The two specimens are extremely different. In the one from Iraq the dorsal scales are rather small and feebly keeled, in the one from Saudi Arabia they are large, strongly imbricate, mucronate, and strongly keeled, the region of relatively large scales extending forwards nearly to the pectoral region. Thus, scales across middle of back for both specimens: 44; 30. Longitudinal series of ventral plates: 10; 8. (In the Arabian specimen there is a gradual transition from lateral scales to ventral plates, which makes the distinction somewhat artificial). Transverse series of ventral plates: 27. Plates in collar: 10; 9. Gular scales in a straight median series: 24; 30. Femoral pores: 23/22; 19/20. Lamellae under 4th toe: 22; 21.

Measurements. Iraq—Snout-vent: 59 mm. Tail: 124 mm. Saudi Arabia—Snout-vent: 94 mm. Tail: 190 mm.

Coloration. The Iraq specimen is typically striped, with about eight light stripes broken up into dots in their anterior parts (the lateral ones more so), and with roundish light spots on the limbs. The Arabian specimen is uniform brown, the keels forming lighter lines.

Acanthodactylus cantoris blanfordi Boulenger

Acanthodactylus cantoris blanfordi Boulenger, 1918, Bull. Soc. Zool. France, 43: 154 (Jask, Iranian Baluchistan, and Bam, Iran).

Material examined. WEST PAKISTAN (2): MCZ 54438–39, Nag, 4000 ft., 75 mi. NE of Panjgur, Baluchistan.

Pholidosis. Scales across the middle of the back: 33; 40. Longitudinal series of ventral plates: 14; 12. Transverse series of ventral plates: 29; 30. Plates in collar: 8; 10. Gular scales in a straight median series: 31; 32. Femoral pores: 17/15; 17/?. Lamellae under 4th toe: 21/19; 23/23.

Measurements. Male (MCZ 54438)—Snout-vent: 60 mm. Tail: 118 mm. Female (MCZ 54439)—Snout-vent: 56 mm. Tail: 105 mm.

Coloration. Indications of light strips on pelvis and tail base. Back of female with rows of dark roundish spots. Hindlimb of both with round light spots, so close that only a reticulum of the dark ground color remains.

Acanthodactylus micropholis Blanford

Acanthodactylus micropholis Blanford, 1874, Ann. Mag. Nat. Hist., (4) 14: 33 (Magas, Baluchistan).

Material examined. WEST PAKISTAN (3): MCZ 54434–35, Saradoo, 28 mi. S of Panjgur, Baluchistan, 27 March 1955. MCZ 54440, Nag, 4000 ft., 75 mi. NE of Panjgur, Baluchistan, 30 March 1955.

Pholidosis. First supraocular broken up into one large and several tiny fragments. Scales across middle of back: 45; 39; 50. Longitudinal rows of ventral plates: 8. Transverse rows of ventral plates: 27; 29; 30. Plates in collar: 10; 10; 9. Gular scales in a straight median series: 33; 28; 31. Femoral pores: 25/26; 24/22; ?/?. Lamellae under 4th toe: 26/27; 24/23; 24/23.

Measurements. Largest male (MCZ 54434)—Snout-vent, 60 mm. Tail: 127 mm. Adpressed hindlimb reaches eye. A juvenile (MCZ 54440)—Snout-vent, 40 mm. Tail, 74 mm.

Coloration. Dorsum of the two adult males dark grey-brown with about ten indistinct, interrupted, narrow, straw-white stripes, which become more striking towards and on the broad base of the tail. The juvenile has eight distinct light stripes from occiput to near the pelvis, where they become reduced in number. Between the two lateralmost stripes (on either side) there are indications of another, indistinct and interrupted, light line. In all specimens the limbs bear roundish light flecks, and on the sides of the head alternating light and dark vertical bars.

Remarks. The number of longitudinal series of ventral plates falls short of the normal figure.

Acanthodactylus scutellatus hardyi Haas
Plate 8, A–C; Plate 12, A

Acanthodactylus scutellatus hardyi Haas, 1957, Proc. Calif. Acad. Sci., (4) 29 (3): 72 (Bir Hirmas Station, N of Tebuk, Saudi Arabia).

Material examined. IRAQ (3): MCZ 56650–52, Lake Habbaniya.

Pholidosis. Suture between internal nasals very short, a quarter, at most, of the length of the frontonasal. Fourth supraocular broken up into granules. No enlarged anterior gulars bordering the chin shields. The whole pileus is only twice as long as broad, and in MCZ 56650 even shorter. Upper labial anterior to center of eye, 5 (but 4/5 in MCZ 56652). Scales across middle of back: about 53; 55; 53. Longitudinal series of ventral plates: 12. Transverse series of ventral plates: 27; 28; 29. Plates in collar: 9. Gular scales in a straight median series: 29; 28; 26. Femoral pores: 19/20; 19/18; 21/?. Lamellae under 4th toe: 20/22; 20/19; 22.

Measurements. Male (MCZ 56651)—Snout-vent: 58 mm. Female (MCZ 56652)—Snout-vent: 56 mm. Both tails broken. (MCZ 56650 is badly contorted.)

Coloration. Hardly discernible, very dark. Male with (or with a remnant of) blackish reticulum on back. Both with light and dark vertical bars on sides of head.

Remarks. This form had been described on the basis of a single specimen from north of Tebuk, northwestern Saudi Arabia. It is both gratifying and interesting to have these extremely similar specimens (meta-

types) from a locality distant more than 800 km towards the northeast. Furthermore, Boulenger's specimen from Basra (1921, 1: 107, last among "forma *typica*") obviously belongs also to *A. s. hardyi*. Certain scale counts of these specimens (including Boulenger's) are at about the lower limit of the range for *A. s. scutellatus* from southern Israel (N=20, personal observation): the number of scales across the middle of the back, longitudinal rows of ventral plates, plates in collar, gular scales, and lamellae under 4th toe. The number of transverse rows of ventral plates does not even overlap (with the samples at hand): *A. s. hardyi* (N=4), 27–29; *A. s. scutellatus* (N=20), 32–36. The number of femoral pores is the same in both forms.

Acanthodactylus tristrami iracensis Schmidt
Plate 9; Plate 12, B

Acanthodactylus tristrami iracensis Schmidt, 1939, Field Mus. Nat. Hist., Zool. Ser., 24 (7): 60–62.

Material examined. IRAQ (4): MCZ 56653–54, ♂♂, 56657–58, ♀♀, Station K-3, near Haditha on the Euphrates.

Pholidosis. Scales across middle of back: 47; 43; 50; 43. Longitudinal rows of ventral plates: 10. Transverse rows of ventral plates: 26; 28; 29; 27. Plates in collar: 9; 10; 10; 10. Gular scales in straight median series: 27; 25; 25; 26. Femoral pores: 21/22; 23/22; 19; 20/21. Lamellae under 4th toe: 23; 22; 23; 23.

Measurements. Largest male (MCZ 56653)—Snout-vent: 57 mm. Tail: 82 mm. Both females—Snout-vent: 56 mm. Tails incomplete.

Coloration. Ground color grey. Vermiform blackish crossbars, irregularly interrupted or confluent, contain whitish round spots, each about three scales in diameter. These white spots are arranged in up to 10 longitudinal rows. Side of head with a dark vertical bar through eye, and blackish spots in temporal area. Limbs and tail mottled grey, blackish, and white (dorsally). All underparts straw-white.

Acanthodactylus cf. *tristrami orientalis* Angel

Acanthodactylus tristrami orientalis Angel, 1936, Bull. Inst. Égypte, 18: 109–110 (Syria: Palmyra, Tell Abiad, Ain Zahra, Deir-ez-Zor).

Material examined. SYRIA (4): MCZ 56660–63, 10 mi. E of Station T-1.

Pholidosis. Three supraoculars, the first broken up into two units in MCZ 56663, and into four in MCZ 56662. The keeled subocular enters the mouth behind the fourth upper labial. Scales across middle of back: 47; 44; 52; 46. Longitudinal series of ventral plates: 10. Transverse series of ventral plates: 31; 30; 28; 26. Plates in collar: 10. Gular scales in a straight median series: 29; 26; 33; 26. Femoral pores: 22; 20; 23; 21. Lamellae under 4th toe: 24; 24; 23; 19. Scales covering fingers in three rows.

Measurements (Largest male, MCZ 56662). Snout-vent: 63 mm. Tail: 86 mm. Neck narrower than head. Adpressed hindlimb reaching between shoulder and ear.

Coloration. Rather dark. Discernible are light round spots, enmeshed in a coarse blackish reticulum which tends to form irregular, oblique, transverse blotches. The light spots form longitudinal rows.

Remarks. If these specimens belong to *A. tristrami*, they certainly represent Angel's subspecies *orientalis*. However, certain details are not in agreement with this determination: the neck is not broad enough for that stout species; the first supraocular is, on the whole, not sufficiently broken up; the pectination of the 4th toe is better developed posteriorly than anteriorly. According to Boulenger's (1921) key, these characters point to *Acanthodactylus micropholis* Blanford, which moreover, has scale counts to rather similar to those of *tristrami* (see also Minton, 1966: 108, 111), but has never been recorded west of southeastern Iran. On the other hand, the length of limbs and tail and the pattern agree better with those of *tristrami* than with those of *micropholis*, and the same is true of the arrangement of

the preanal plates. Angel's (1936) short description of *A. t. orientalis* contains no information on the dubious points raised here. Thus apparently our specimens indeed belong to the same population as Angel's, whatever their real affinities may be.

Acanthodactylus robustus (F.) Werner
Plate 10; Plate 12, C

Acanthodactylus robustus Werner, 1929, Zool. Anz., 81 (7/10): 240–242, fig. 2 (Syrian Desert at Bir Molusi [Meloza], [Qaara Depression] between Damascus and Baghdad).

Material examined. SYRIA (3): MCZ 56645, ♀, from Qariatein to IPC Pipeline; MCZ 56648, ♀, and 56649, ♂, 20 mi. N of Station T-2.

Pholidosis. Three supraoculars, the first broken up into one large and a few minute fragments. Subocular separated from mouth by the 5th (or 5th and 6th) supralabials. Upper temporals, a large one succeeded by a small one. Scales across middle of back: 56; 57; 55. Longitudinal series of ventral plates: 10. Transverse series of ventral plates: 28; 29; 27. Plates in collar: 8; 9; 10. Gular scales in a straight median series: 31; 26; 27. Femoral pores: 21/20; 19/22; 27/29. Lamellae under 4th toe: 21/23; 18/19; 23/25.

Measurements. Male—Snout-vent: 69 mm. Tail: 49+5 mm. Larger female (MCZ 56648)—Snout-vent: 66 mm. Tail: 66 mm.

Coloration. MCZ 56648 resembles the photograph, evidently also a female, given by F. Werner. In the male there is a tendency for the light spots, on both back and tail, to form light crossbands. This tendency is carried further in the other female (MCZ 56645), where the tail has dorsal semi-regular crossbands.

Remarks. F. Werner, in his description, states that the closest relationship of *A. robustus* is with *A. grandis* (Werner, 1929: 240). As a matter of fact, *robustus* differs greatly from *grandis* in its habitus and proportions, as well as in the arrangement (not merely the number) of ventral plate rows. The apparent relation to *grandis* follows from the use of Boulenger's key (1921), which is based on superficial characters.

Acanthodactylus grandis Boulenger
Plate 11; Plate 12, D

Acanthodactylus grandis Boulenger, 1909, Ann. Mag. Nat. Hist., 4 (8): 189 (Jerud and Ataiba, Syria).

Material examined. SYRIA (2): MCZ 56644, ♂, from Qariatein to IPC Pipeline; MCZ 56647, ♀, 3 mi. NW of Station T-2, 11 March 1950.

Pholidosis. Scales across middle of back: 55; 57. Longitudinal series of ventral plates: 14. Transverse series of ventral plates: 30. Plates in collar: 11. Gular scales in a straight median series: 28; 29. Femoral pores: 22; 18/16. Lamellae under 4th toe: 21/23; 21.

Measurements. Male—Snout-vent: 65 mm. Female—Snout-vent: 87 mm. Both tails broken.

Coloration. The male shows no discernible pattern, but the female has at least eight longitudinal rows of dark round spots, five to seven scales in diameter.

Remarks. The large female is not of maximum size (Boulenger, 1921: 115).

Ophisops elegans sspp.
Tables 2, 3; Figure 5

Ophisops elegans Ménétriés, 1832, Cat. Rais. Obj. Zool. . . . Voy. Caucase . . . , p.63 (near Baku, Transcaucasus, U. S. S. R.).

Ophisops elegans varieties *typica, ehrenbergii, mizolepis,* and *persicus,* Boulenger, 1921, Monograph of the Lacertidae, Vol. 2, London, pp. 211–222.

Ophisops elegans elegans Lantz, 1931, Bull. Mus. Géorgie, Tiflis, 6: 34.

Ophisops blanfordi Schmidt, 1939, Field Mus. Nat. Hist., Zool. Ser., 24 (7): 64–65 (Halfaya, 20 mi. E of Amara, Iraq).

Material examined. IRAQ (52): MCZ 56672–80, 56682–91, Kish area; MCZ 56681, Afaq; MCZ 56809–28 (and 12 unnumbered specimens), probably from Kish area. IRAN (93): MCZ 56692, Mazuo; MCZ 56694–56748, Shalgahi; MCZ 56749, Mahor

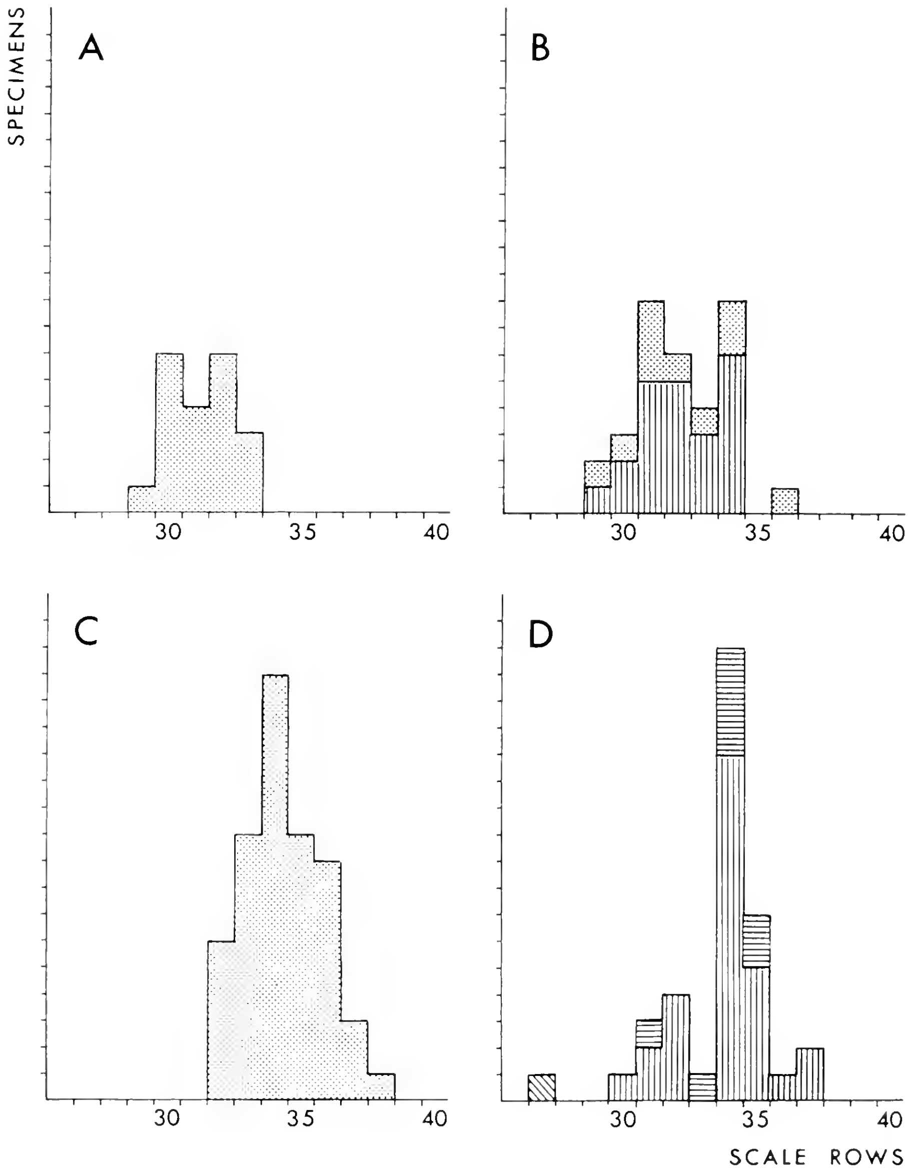


Figure 5. Variation in the number of scales around the middle of the body in population of *Ophisops elegans*. The hatching, in any direction, denotes the presence of two postnasals (on each side), whereas the stippling denotes the presence of a single postnasal (on one or both sides).

A, Iraq: Kish area and Afaq.

B, "Iraq," probably Kish area.

C, Iran: Shalgahi.

D, Iran: Dorud and Mazuo—vertical hatching; Zogheh—horizontal hatching; Mahor Birinji—diagonal hatching.

TABLE 2. VARIATION IN SCALE COUNTS IN *OPHISOPS ELEGANS* SSPP.
(N = number of specimens, O.R. = observed range, M = mean, S.D. = standard deviation.)

Material		Scales around middle of body			Femoral pores			Lamellae under 4th toe			
Locality	N	O.R.	M	S.D.	O.R.	M	S.D.	O.R.	M	S.D.	Post-nasals
Iraq											
Kish area	19	29–33	31.1	1.15	10–12	11.3	0.24	23–27	25.1	1.29	1
Afaq	1	33			12			23			1
"Iraq," probably Kish area	32	29–36	32.2	1.72	9–12	10.9	0.28	22–27	24.3	1.31	1–2
Iran											
Shalgahi	55	32–38	34.3	1.47	10–14	11.3	0.28	22–27	24.8	1.24	1
Mazuo	1	32			11			24			2
Mahor Birinji	1	27			10			23			2
Zagheh	8	31–35	33.8	1.28	10–13	11.3	0.30	23–26	24.1	0.31	2
Dorud	28	30–37	33.8	1.68	9–14	11.6	1.06	22–26	23.8	1.09	2

Birinji; MCZ 56750–57, Zagheh; MCZ 56758–60, 56752–68, 56770–87, Dorud.

Pholidosis. The number of postnasals varies as follows. All specimens from the Kish area and the relatively nearby Afaq, as well as all specimens from Shalgahi in Iran, have one postnasal. All remaining specimens from Iran (Mazuo, Mahor Birinji, Zagheh, Dorud) have two postnasals (on each side), with the exception of a single specimen (MCZ 56756), which has only one very small postnasal on each side. The series marked only "Iraq," but probably from the Kish area, includes 22 specimens with two postnasals, four with a single postnasal, and six that are asymmetrical in this respect. The occipital is small, or very small, in all specimens from Iraq, and also in those from Shalgahi, with the exception of one (MCZ 56734), which has a relatively large occipital and an additional interparietal. The specimens from Mazuo, Mahor Birinji, Zagheh, and Dorud have a relatively broad occipital. Pertinent meristic characters are summarized in Tables 2 and 3.

Measurements. Specimens from the Kish area, Afaq, and Shalgahi reach 48–50 mm

TABLE 3. VARIATION IN THE EXTENT OF THE VERTEBRAL LINE IN *OPHISOPS ELEGANS* SSPP.

Material		Number of specimens					
		Without vertebral line	With a vertebral line from occiput to				
Locality	N		Occiput	Shoulder	Midbody	Pelvis	Tail base
Iran							
Kish area	19	12	4	3	0	0	0
Afaq	1	0	1	0	0	0	0
"Iraq," probably Kish area	32	5	5	11	7	4	0
Iraq							
Shalgahi	55	20	20	14	1	0	0
Mazuo	1	1	0	0	0	0	0
Mahor Birinji	1	0	1	0	0	0	0
Zagheh	8	1	4	3	0	0	0
Dorud	28	19	9	0	0	0	0

(except for one specimen of 53 mm) in snout-vent length; the remaining specimens from Iran reach 52–54 mm; in the series marked "Iraq," probably from the Kish area, the largest specimens are 47–48 mm.

Coloration. The degree of development of the dark vertebral line, which in Jordan facilitates distinction between *O. elegans* sspp. and *O. blanfordi* Schmidt (being well developed only in the latter [Y. L. Werner, in MS]), is very variable in the present material. In the series from most localities it is little developed, so that in most specimens it is absent or present only as a short (occipital) line, not reaching the shoulders. It is somewhat better developed in the series from Shalgahi, reaching the shoulder in several specimens. It is best developed in the series labeled "Iraq" (probably from the Kish area), even reaching the pelvis in some specimens. The details of this variation are presented in Tables 2 and 3.

Remarks. Ophisops elegans (*sensu lato*) comprises a group of forms well known for the taxonomic difficulties posed by its variation. It appears that some of the salient variable characters present their own independent geographic variation, so that the various characters formerly used to distinguish any subspecies do not necessarily coincide geographically. Thus our specimens from the Kish area (and Afaq) correspond in their single postnasal, small occipital, and number of scale rows to Boulenger's variety *mizolepis*, which was redescribed by Schmidt as *Ophisops blanfordi*. But the animals from Shalgahi, also with a single postnasal and a small occipital, have higher counts of scale rows. The specimens from Mazuo, Mahor Birinji, Zagheh, and Dorud resemble Boulenger's variety *persicus* (synonymized with *O. e. elegans* by Lantz) in most respects, including the relatively broad occipital, but have a somewhat higher count of femoral pores. Of special interest are the 32 specimens that unfortunately are labeled only "Iraq," but that are probably from the Kish area, and that vary in the number of postnasals. The high percentage of asymmetrical specimens tends to confirm that this is indeed a series of either transitory or hybrid nature (and not mixed from different localities). The remaining characters place this series between Schmidt's *O. blanfordi* and Boulenger's variety *ehrenbergi*, which was synonymized by Lantz with *O. e. elegans.* But for the element of uncertainty introduced by the absence of an exact locality, this would be a demonstration of intergradation between *O. blanfordi* and *O. elegans*, which, according to Schmidt (1939: 65), would reduce *O. blanfordi* to subspecific rank.

Eremias guttulata guttulata (Lichtenstein)
Table 4; Figures 6, A; 7, A

Lacerta guttulata Lichtenstein, 1823, Verz. Doubl. Mus. Berlin, p. 101 (Egypt).
Eremias guttulata: A. Smith, 1845, Ill. Zool. S. Afr., Rept., pl. 48, fig. 8.
Eremias guttulata forma *typica:* Boulenger, 1921, Monograph of the Lacertidae, Vol. 2, London, p. 258.
Eremias guttulata guttulata: Wettstein, 1928, Sitzungsber. Akad. Wiss. Wien, Math.-Naturw. Kl., Abt. 1, 137 (10): 782.

Material examined. IRAQ (4): MCZ 56630–32, Station K-3, near Haditha; MCZ 56633, Qaara Depression (NW of Station H-2). SAUDI ARABIA (7): MCZ 56634–39, 56641, between Al-Gaisumah and Turaif on Tapline.

Pholidosis. Invariably four upper labials in front of the subocular and four more behind it (the same is true of specimens from southern Israel—personal observation). In comparison with specimens of *E. g. guttulata* from Israel, all specimens have the pileus rather flattened, owing to the much reduced elevation of the eyes and, especially, the nostrils; the caudal scales are very strongly carinated. The variation of meristic characters is summarized in Table 4.

Measurements (largest specimen, MCZ 56635). Snout-vent: 53 mm. Almost all others are between 48 and 50 mm.

Coloration. All specimens have a rather

TABLE 4. VARIATION IN SCALE COUNTS IN *EREMIAS GUTTULATA* SSPP.
(N = number of specimens, O.R. = observed range, M = mean, S.D. = standard deviation.)

Material		Scales across middle of back			Ventral plates: number of						Plates in collar			Gular scales in straight median series			Femoral pores			Lamellae under 4th toe		
					Longitudinal series			Transverse series														
Locality	N	O.R.	M	S.D.	O.R.	M	S.D.	O.R.	M	S.D.	O.R.	M	S.D.	O.R.	M	S.D.	O.R.	M	S.D.	O.R.	M	S.D.
Iraq	4	41–46	43.0		10–11	10.3		29–30	29.8		13–15	13.5		25–28	25.8		13–14	13.8		20–23	21.0	
Arabia	7	40–50	43.6	3.64	10	10.0	0	29–34	30.6	1.90	10–14	12.4	1.51	25–30	27.9	2.85	13–15	14.0	0.76	21–24	22.1	1.21
Iraq plus Arabia	11	40–50	43.1	3.29	10–11	10.1	0.30	29–34	30.3	1.55	10–15	12.8	1.40	25–30	27.1	2.30	13–15	13.9	0.68	20–24	21.7	1.35
Iran	9	40–50	45.4	3.40	10–12	10.3	0.22	26–33	31.3	2.18	9–15	12.2	1.99	21–26	23.0	1.41	10–13	11.8	0.83	21–26	23.1	1.62
West Pakistan	2	40–42	41.0		10	10.0		29–31	30.0		11–12	11.5		23–26	24.5		10–13	11.8		22–23	22.5	
Iran plus West Pakistan	11	40–50	44.6	3.56	10–12	10.3	0.65	26–33	31.1	2.07	9–15	12.1	1.81	21–26	23.3	1.56	10–13	11.8	0.93	21–26	23.0	1.49

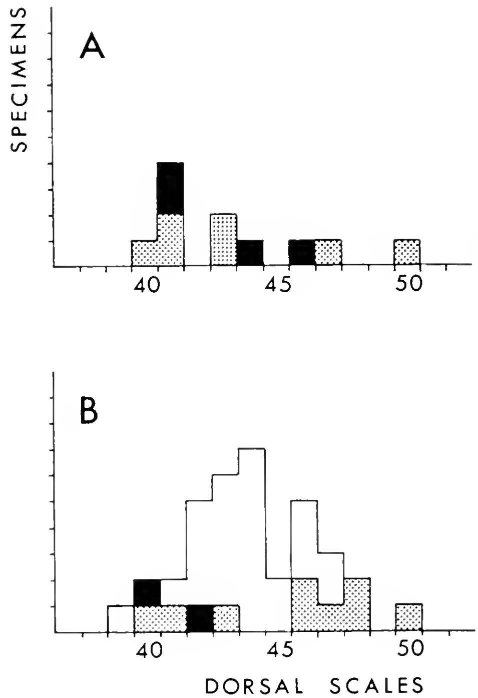


Figure 6. Variation in the number of scales across the middle of the back in subspecies of *Eremias guttulata*.

A, *E. g. guttulata*: Iraq—black; Saudi Arabia—stippled.

B, *E. g. watsonana*: Iran—stippled; Iran—25 specimens from S. C. Anderson, 1963—white; West Pakistan—black.

indistinct pattern of ocelli, which, perhaps, is not an artifact of preservation. There is a tendency for the dark margin to be accentuated on both lateral sides of each light spot.

Eremias guttulata watsonana Stoliczka
Table 4; Figures 6, B; 7, B

Eremias (*Mesalina*) *watsonana* Stoliczka, 1872, Proc. Asiat. Soc. Bengal, p. 86 (Sind, between Karachi and Sukkur).

Eremias guttulata watsonana: Smith, 1935, Fauna Brit. India, Rept. Amphib., 2: 389.

Material examined. IRAN (9): MCZ 56607, 56609, 56616, 56619–20, 56626–29, Mahor Birinji. WEST PAKISTAN (2): MCZ 54436, ♂, Saradoo, 28 mi. S. of Panjgur, Baluchistan, 27 March 1955; MCZ

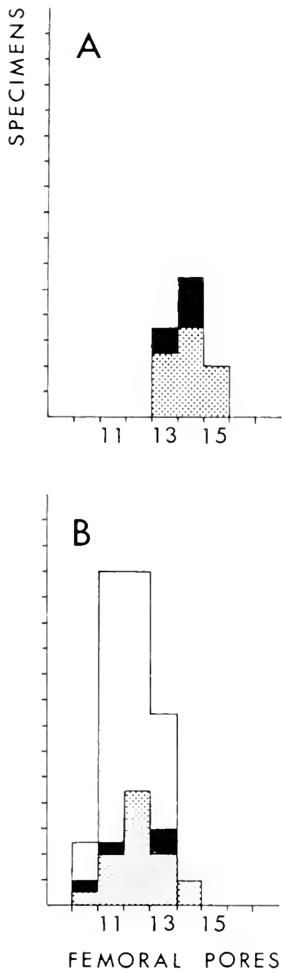


Figure 7. Variation in the number of femoral pores in subspecies of *Eremias guttulata*.
A, *E. g. guttulata:* Iraq—black; Saudi Arabia—stippled.
B, *E. g. watsonana:* Iran—stippled; Iran—25 specimens from S. C. Anderson, 1963—white; West Pakistan—black.

54437, ♂, Nag, 4000 ft., 75 mi. NE of Panjgur, Baluchistan, 30 March 1955.

Pholidosis. In all cases, four upper labials in front of the subocular, and only three behind it. In three specimens there are two successive occipitals behind the interparietal (MCZ 56607, 56627–28). In both specimens from West Pakistan, the window in the lower eyelid is formed by two large scales (the vertical seam in between being black), beneath which are several smaller scales. In the specimens from Mahor Birinji, the scales of the window are somewhat variable. The variation of meristic characters is summarized in Table 4.

Measurements. Two largest specimens from Iran—Snout-vent: 57 mm, 58 mm (several others measure 54–55 mm). Two specimens from West Pakistan—Snout-vent: 45 mm, 44 mm.

Coloration. Quite indistinguishable.

Remarks. Smith (1935: 389–90) re-established the subspecies *watsonana,* in contradistinction with Boulenger (1921, 2: 258), who had united it with his forma *typica.* Our specimens are listed under *watsonana,* in spite of certain deviations, mainly on account of the very distinct and completely free collar. The same course has been generally adopted by recent authors. According to S. C. Anderson (1963: 460), " . . . *watsonana* is known from Iran, Afghanistan, West Pakistan, and northwest India"; according to Minton (1966: 110), " . . . *watsonana* occurs from Rajputana to southern Afghanistan and westward to Syria and northern Arabia, intergrading with the nominate race around the northern end of the Red Sea." Since we have the impression that there is a gradual cline, in several respects, from east to west, such that specimens from western Iran (including those listed here), Iraq, and Jordan are more or less intermediate between the two forms, we preferred to follow the convention of regarding the more western populations as belonging to *E. g. guttulata.*

Eremias olivieri ssp.

Lacerta olivieri Audouin, 1829, Descr. Egypte, Rept., Suppl., p. 175, pl. 2, fig. 1 (Egypt, Sinai, or Palestine—Haas, 1951b: 275).

Eremias olivieri: Haas, 1951, Copeia, 1951 (4): 274–276.

Material examined. SAUDI ARABIA (1): MCZ 56640, between Al-Gaisumah and Turaif on Tapline.

Pholidosis. Scales across the middle of the back, 40. Longitudinal series of ventral

plates, 10. Transverse series of ventral plates, 31. Plates in collar, 12. Gular scales in straight median series, 30. Femoral pores, 13/14. Lamellae under 4th toe, 21. On one side, four upper labials preceding the subocular (which enters the mouth), on the other, five. On either side, four upper labials behind the subocular. Scales under the basal portion of the tail (the distal portion is missing) convex or bluntly keeled.

Measurements. Snout-vent: 44 mm.

Coloration. A distinct impression of a longitudinal striping is created by a pair of dorsolateral longitudinal rows of light spots (each about 4 scales in diameter), each of which is bordered along its medial side by a blackish longitudinal line, about five scales long (and 1 broad). On either side of this pair of bicolored interrupted bands are small scattered ocelli, and less distinct ocelli are in evidence dorsally, between the two bands. Along each flank runs a light band (starting at the subocular), two to three scales broad, and one scale removed from the lateral series of ventral plates.

Remarks. Haas (1951b) discussed the independent status of *Eremias olivieri* and defined it as a species. It is not possible to determine our single specimen at the subspecific level. That this specimen was collected in the same general locality as the series of *E. guttulata guttulata* shows that apparently in northwestern Arabia, as in certain areas of southern Israel, the two may be sympatric (Haas, 1951b). *E. olivieri* has been collected in Jordan (Haas, 1951a), but apparently has not so far been identified from Iraq (Khalaf, 1959) or Arabia.

Eremias brevirostris brevirostris (Blanford) Table 4; Figures 8–12; Plates 13–15, Plate 18, C–F

Mesalina brevirostris Blanford, 1874, Ann. Mag. Nat. Hist., (4) 14: 32 (Kalabagh, Punjab, and Tumb Island, Persian Gulf—restricted to Kalabagh by Schmidt, 1939: 66).

Eremias brevirostris: Boulenger, 1887, Cat. Lizards Brit. Mus., 3: 87.

Eremias brevirostris forma *typica:* Angel, 1936, Bull. Inst. Egypte, 18: 111–112.

Material examined. SYRIA (3): MCZ 56586, from Qariatein to IPC Pipeline; MCZ 56586, Wadi Sukhura near Jebel Abdul Aziz; MCZ 56587, 20 mi. N of Station T-2. IRAQ (13): MCZ 56588–92, Lake Habbaniya; MCZ 56593, Afaq; MCZ 56621–23, Qaara Depression N of Rutba. SAUDI ARABIA (20): MCZ 56565–84, between Al-Gaisumah and Turaif on Tapline. BAHRAIN ISLAND: MCZ 54441, 6 mi. S of Zallaq, 21 March 1955. WEST PAKISTAN: MCZ 54442, Pasni, Baluchistan.

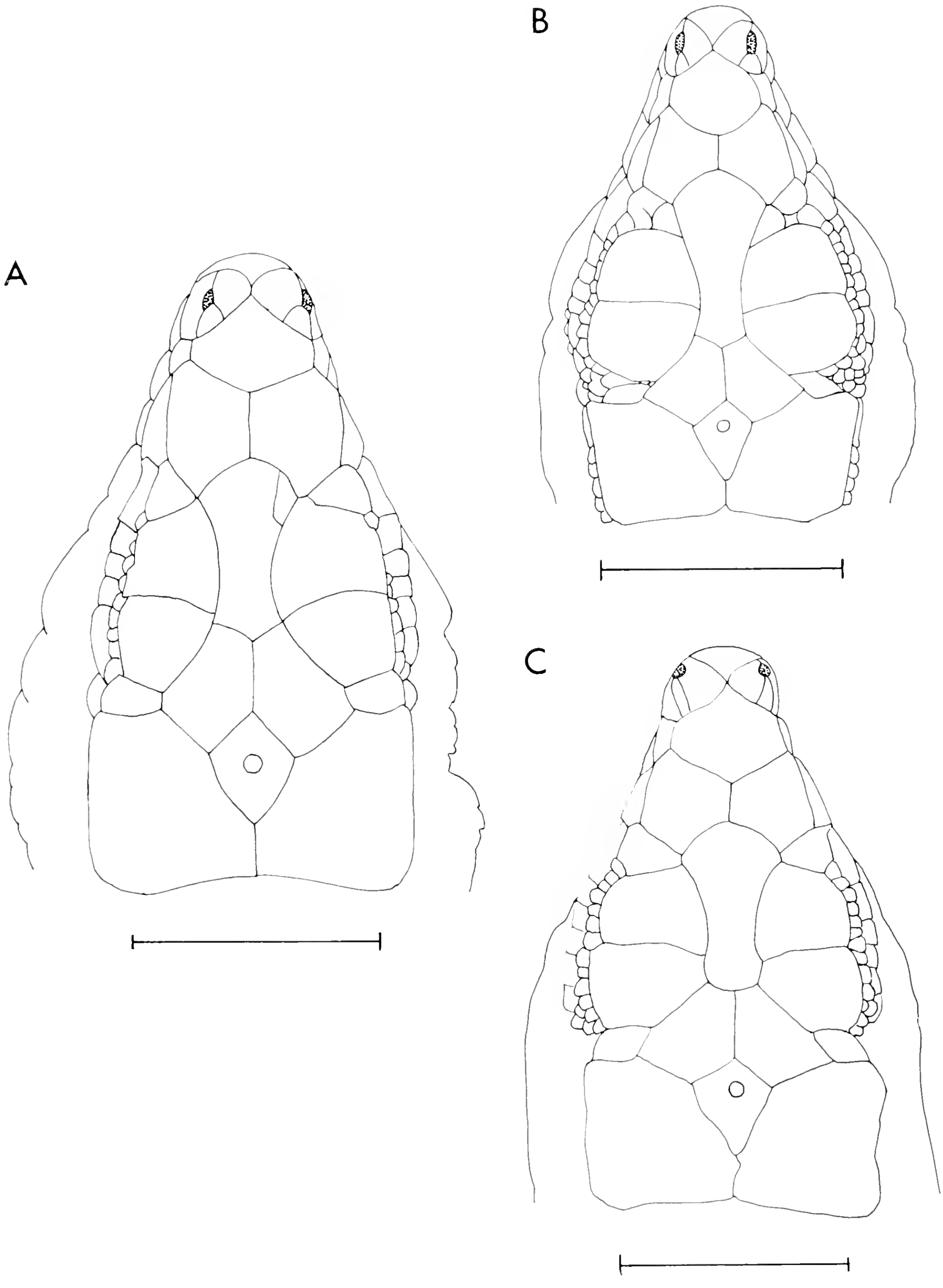
Pholidosis. The arrangement of the upper labials and their relation to the subocular varies as follows. *Syria:* the subocular enters the mouth in one case (MCZ 56586—behind the 4th labial on the left side, behind the 3rd on the right); in two cases it is separated from the mouth (MCZ 56585—by the 5th labial; MCZ 56587—by the small 5th and 6th labials). *Iraq:* the subocular enters the mouth in only three cases (MCZ 56592–93, 56622)—always behind the 4th labial; it is separated from the mouth in nine cases — in seven of these by the 5th labial (MCZ 56588–89, 56621, 56623–25, 56655); in one case asymmetrically by the 5/6th labial (MCZ 56591); in one case symmetrically by the small 6th and 7th labials (MCZ 56590). One specimen (MCZ 56656) is asymmetrical in that the subocular enters the →

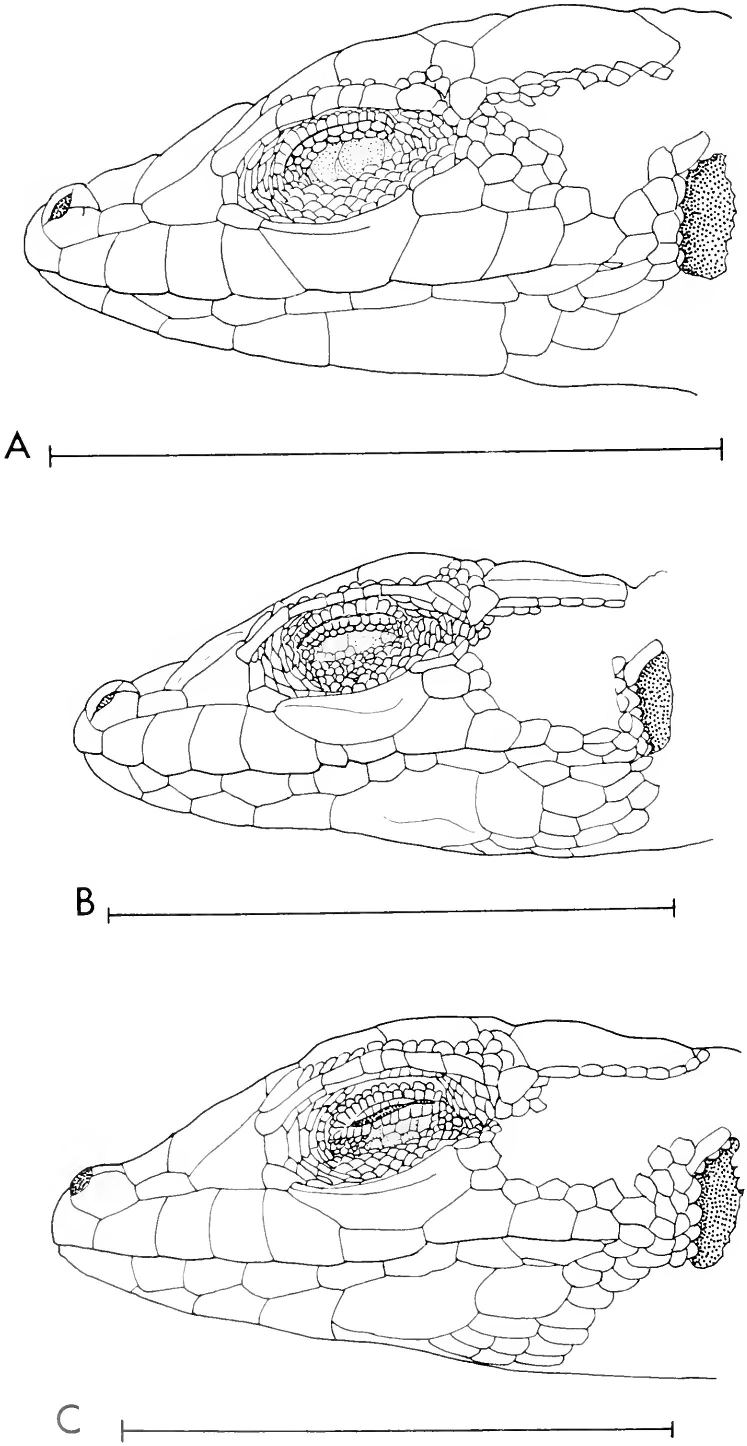
Figure 8. *Eremias brevirostris* sspp. Head, dorsal view, of:

A, *E. b. fieldi* subspec. nov., MCZ 56617, ♂, type, from Iran (Mahor Birinji).

B, *E. b.* cf. *brevirostris*, MCZ 56570, from Arabia (between Al-Gaisumah and Turaif).

C, *E. b.* cf. *microlepis*, HUJ-R 6183, from Jordan (Amman—Chissa). Scale bars: 5 mm.


A
B
C


A
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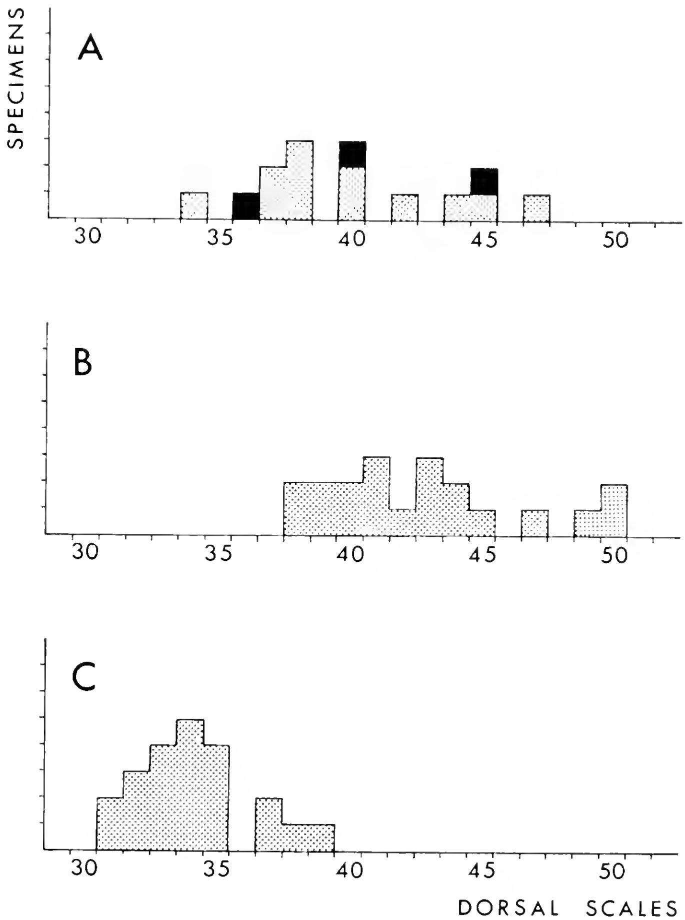

Figure 10. Variation in the number of scales across the middle of the back in subspecies of *Eremias brevirostris*.
A, *E. b. brevirostris*: Syria—black; Iraq—stippled.
B, *E. b.* cf. *brevirostris* from Arabia.
C, *E. b. fieldi* subspec. nov. from Iran (Mahar Birinji and Gotwand).

mouth on the left side (behind the 5th labial), but not on the right, where it is separated from the mouth by the 5th labial (MCZ 56656).

Measurements. Snout-vent lengths of the largest specimens from the various localities are as follows. *Syria:* 50 mm (MCZ 56586). *Iraq:* Lake Habbaniya, 60 mm (MCZ 56592); Afaq, 53 mm (MCZ 56593); all five specimens from Station K-3 near Haditha: 50–52 mm; Qaara Depression, 48 mm (MCZ 56624). *Saudi Arabia:* 48 mm (MCZ 56572). *West Pakistan:* both 40–42 mm (contorted). (For comparison.

←

Figure 9. *Eremias brevirostris* sspp. Head, lateral aspect, of:
A, *E. b. fieldi* subspec. nov., MCZ 56610, ♂, paratype, from Iran (Mahar Birinji).
B, *E. b.* cf. *brevirostris*, MCZ 56570, from Arabia (between Al-Gaisumah and Turaif).
C, *E. b.* cf. *micralepis*, HUJ-R 6183, from Jordan (Amman—Chisso). Scale bars: 10 mm.

the largest of the types listed by Boulenger [1921] from Kalabagh was 44 mm; on the other hand, specimens from Transjordan [Jordan] reach 57 mm [HUJ-R 1229].)

Coloration. In most of the specimens the pattern is not well preserved. Nevertheless it is evident that the basic pattern of ocelli is very variable. Thus in MCZ 56656 there are four regular longitudinal rows of ocelli, each with a light center about three scales wide, and a dark margin two to three scales broad. The margin of each light spot is particularly well developed cranially and caudally, so that there is a tendency for the formation of longitudinal dark chains. In other specimens (e.g., MCZ 56592) the light spots are not so regularly disposed, and the black margin is better developed on both lateral sides of each light spot. The two specimens from West Pakistan are rather light colored, with only a pair of delicate dark dots flanking each white spot on its lateral sides.

Remarks. Eremias brevirostris ranges from Syria to northwestern India. Considerable geographic variation is evident in our material (Table 5). There seem to be sufficient grounds for considering our material from Iran as a distinct subspecies (see *Eremias brevirostris fieldi* subsp. nov.). Specimens from Arabia probably also represent a distinct population, characterized by, among other things, a very pointed snout and a tendency for a higher number of upper labials. However, our series is too variable for the formal definition of a distinct subspecies.

Blanford's types were from Kalabagh (Punjab) and Tumb Island (Persian Gulf); Schmidt (1939: 66) restricted the type locality to Kalabagh. Counts of Blanford's four types, from Boulenger (1921), are appended to our Table 5, for comparison. Our specimens from West Pakistan, both in bad condition, resemble Boulenger's (1921) specimen from Dasht (Baluchistan). Counts of all three accord fairly well with those of the types. In our Pakistan specimens the snout is pointed, the nostril not swollen, the naris a horizontal slit between the two larger nasals (out of three) and hardly visible.

The specimens from Iraq are not distinguishable on the basis of scale counts from the typical population of the Punjab and West Pakistan; unless geographical discontinuity be proved, they may be regarded as belonging to the typical subspecies. Head shape in the Iraq specimens, however, varies considerably. In the single specimen from Afaq the head is flat, the nostrils very moderately elevated. In specimens from Lake Habbaniya the head is blunt and wedge-shaped, with swollen nostrils. The head is higher than in specimens from Jordan (in the Hebrew University collection); its plates are smooth, not rugose as in those from Jordan. Specimens from the Qaara Depression (north of Rutba in western Iraq) resemble those from Jordan, but are smaller (see measurements).

The three specimens from eastern Syria, like those from Iraq, appear assignable to *E. b. brevirostris.* Angel (1936), too, while describing *E. b. microlepis* from Haouarine (between Homs and Qariatein), assigned Syrian specimens from Palmyra and northwards to the typical form.

Eremias brevirostris fieldi subsp. nov.

Table 5; Figures 8–12; Plates 16, 17, Plate 18, A, B

Holotype. MCZ 56617, ♂, Mahor Birinji, southwestern Iran.

Paratypes (21). MCZ 56605, 56606, 56608, 56610–15, 56618, from the type locality. MCZ 56594–56604, from 4 mi. W of Gotwand, Iran.

Diagnosis. Differs from *Eremias brevirostris brevirostris* (Blanford) 1874 in its larger scales, the ventrals excepted. Scales across middle of back: 30–39 (usually 33–35). Gular scales in a straight median series: 20–25. Lamellae under 4th toe: 16–20. Femoral pores: mode 12, but up to 15 (see Table 5).

Description of holotype. A male. Head

TABLE 5. VARIATION IN SCALE COUNTS IN *EREMIAS BREVIROSTRIS* SSPP.
(N = number of specimens, O.R. = observed range, M = mean, S.D. = standard deviation.)

Material		Scales across middle of back			Ventral plates: number of Longitudinal series			Ventral plates: number of Transverse series			Plates in collar			Gular scales in straight median series			Femoral pores			Lamellae under 4th toe		
Locality	N	O.R.	M	S.D.	O.R.	M	S.D.	O.R.	M	S.D.	O.R.	M	S.D.	O.R.	M	S.D.	O.R.	M	S.D.	O.R.	M	S.D.
Syria	3	36–45	40.3		12	12		32–34	33		9–11	10		24–27	25.3		14–17	15.5		20–23	21	
Station K-3	5	34–47	40.2		12	12		29–34	31.2		10–12	11.2		23–27	25.4		15–19	16.5		21–23	21.8	
Qaara	2	42–45	43.5		12	12		29–30	29.5		11–12	11.5		23	23		13–14	13.5		23	23	
Syria, K-3, plus Qaara	10	34–47	40.9	4.38	12	12	0	29–34	31.4	1.9	9–12	10.9	0.31	23–27	24.9	1.59	13–19	15.6	1.76	20–23	21.8	1.23
Habbaniya	5	37–40	38.6		12	12		30–36	33		9–11	9.8		21–27	24.6		13–15	13.8		19–23	20.6	
Afaq	1	38			12			33			8			26			16			22		
Habbaniya plus Afaq	6	37–40	38.5	1.22	12	12		30–36	33	2	8–11	9.5	1.05	21–27	24.8	2.40	13–19	14.2	1.17	19–23	20.8	1.72
Arabia	20	38–50	42.9	3.76	10–12	11.5	0.76	30–35	32.6	1.03	6–13	8.6	1.73	22–30	26.1	2.12	12–16	13.5	1.14	21–28	23.3	1.97
Gotwand	11	31–38	33.8	2.5	10–12	11.8	0.6	28–35	31.5	2.07	8–12	9.9	1.04	20–25	22.4	1.57	12–15	13.0	0.96	16–20	18.0	1.18
Mahor Birinji	11	32–39	34.5	2.08	10–12	11.8	0.6	30–35	32.8	1.86	8–12	10.2	1.17	20–24	22.0	1.48	12–14	12.7	0.72	16–18	17.5	0.69
Iran	22	31–39	34.1	2.14	10–12	11.8	0.59	28–35	32.2	2.06	8–12	10	1.09	20–25	22.2	1.50	12–15	12.9	0.85	16–20	17.8	0.53
West Pakistan	2	42	42		10–12	11		29–30	29.5		10	10		28–29	28.5		12–16	14.0		22–23	22.5	
TYPES	4	45–47	46		12	12		30–33	31.8		8–9	8.8		25–28	26.0		14–16	14.9		20–24	21.8	

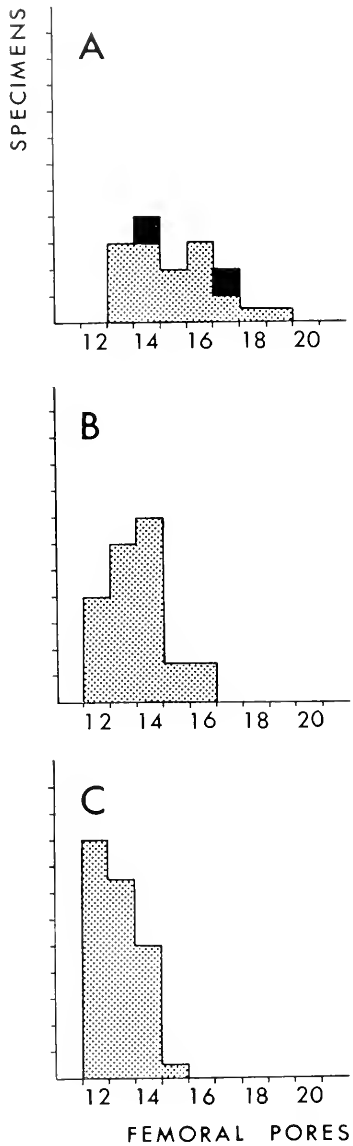

Figure 11. Variation in the number of femoral pores in subspecies of *Eremias brevirostris*.
A, *E. b. brevirostris*: Syria—black; Iraq—stippled.
B, *E. b.* cf. *brevirostris* from Arabia.
C, *E. b. fieldi* subspec. nov. from Iran (Mahor Birinji and Gotwand).

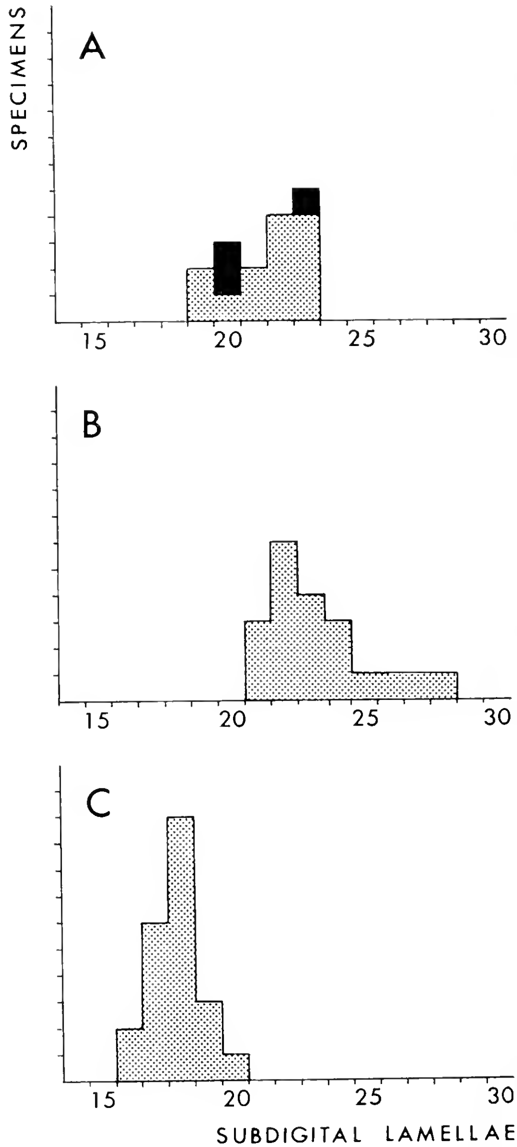

Figure 12. Variation in the number of subdigital lamellae in subspecies of *Eremias brevirostris*.
A, *E. b. brevirostris*: Syria—black; Iraq—stippled.
B, *E. b.* cf. *brevirostris* from Arabia.
C, *E. b. fieldi* subspec. nov. from Iran (Mahor Birinji and Gotwand).

(to rear border of ear) slightly more than one and one half times as long as broad. Nostril not swollen; the opening elongated, nearly twice as long as broad. All upper head shields strongly convex; rugose. Parietals in good sagittal contact behind the interparietal, the line of contact two-fifths of the length of the parietals. No occipital.

Four supraoculars, the second the largest. Subocular longitudinally keeled, entering the mouth as broadly as the 4th upper labial, which precedes it. Behind the subocular two enlarged labials, each about the size of the 4th. Temporal scales roundish, convex, relatively large: only six in a vertical line from pileus to supralabials, half way between eye and ear; only three between pileus and tympanic shield. Lower labials: 6, the last considerably elongate. Chin shields: 5/6, the first 2/3 in contact sagittally. Gular scales in a straight median series: 22. Plates in collar: 9. Thirty-two scales across the middle of the back. Ventral plates in 12 longitudinal series and in 32 transverse series. Femoral pores: 12/13. Lamellae under 4th toe: 19/18. Upper caudal scales (end of original portion) feebly keeled, lower smooth. Tail base very strongly swollen, so that it is as broad as the body just before the pelvis. The swollen region is nearly as long as the trunk between the limbs (interlimb length). Most of the swollen part is covered by the regular large caudal scales, only its anterior third by the smaller scales typical of the base of the tail.

MEASUREMENTS OF HOLOTYPE

	MM
Snout-vent	58.0
From snout to forelimb	22.0
Head length (to posterior border of ear)	13.5
Head width . . .	9.0
Head depth . . .	7.0
Forelimb	16.5
Hindlimb	26.0
Tail	22.0 + 45.0

Coloration of holotype. Very dark, pattern difficult to distinguish. There are indications of ocellus-like spots, the light center about three scales in diameter, the darker rim one to two scales broad. At least some of these ocelli are confluent with their neighbors, forming dark crossbands.

Variation of the type series. In the specimens from Gotwand the nostril may be slightly swollen, and the opening is usually less elongated than in those from Mahor Birinji. The occipital, usually absent, may be represented by one or two minute granules. The first supraocular is rarely divided in two. In one specimen there are only three upper labials in front of the subocular, on one side (MCZ 56613). The number of temporal scales between pileus and upper labials may be six or seven, between pileus and tympanic shield, three or four.

In specimens with complete tails, the part behind the basal swelling has keeled scales dorsally, smooth ones ventrally. Data for the meristic characters are given in Table 5.

Some of the specimens show the pattern described for the holotype somewhat more distinctly. The light spots are arranged in semi-regular longitudinal series. The degree of confluency among their black frames is very variable. On the tail, the pattern gradually changes to one of alternating light and dark half-rings. There seems to be no distinctive pattern on the side of the head; it is either unicolor or somewhat mottled.

Remarks. It is interesting to note that this relatively large-scaled local subspecies occurs in the eastern part of the range of the species, while at the western margin of the range there occurs the small-scaled *E. b. microlepis* Angel (western Syria and northern Jordan—Y. L. Werner, in MS).

Family Scincidae

Eumeces zarudnyi Nikolski

Eumeces zarudnyi Nikolski, 1899, Ann. Zool. Mus. Acad. Sci. St. Petersburg, 4: 399 (Seistan and Kirman in eastern Persia).

Eumeces zarudnyi Nikolski, 1899, Yearb. Zool. Mus. Acad. Sci. St. Petersburg, 4: 400.

Material examined. WEST PAKISTAN (2): MCZ 54443, ♂, Shahi-Tump at Turbat, Baluchistan, 21 March 1955, Chugtai; MCZ 54444, ♂, Saradoo, 28 mi. S of Panjgur, Baluchistan, 27 March 1955, H. Field.

Pholidosis. Both specimens have 28 scale rows (as also mentioned by Taylor for a specimen from Baluchistan), the two mid-dorsal ones being the broadest. The heel plates are distinct in MCZ 54444, smaller in 54443.

Measurements (Largest, MCZ 54444). Snout-vent: 117 mm.

Mabuya aurata septemtaeniata Reuss

Euprepis septemtaeniatus Reuss, 1834, Mus. Senckenb., 1: 47, pl. 3, fig. 1 (Massawa [Massaua]).
Mabuya aurata septemtaeniata: Mertens, 1924, Abh. Ber. Mus. Nat.- Heimatk. (Naturk. Vorgesch.) Magdeburg, 3: 377.

Material examined. IRAQ (11): MCZ 56539–43, 56546, 56548, 56549, Kish area; MCZ 56559–60, Station K-3, near Haditha on the Euphrates. IRAN (8): MCZ 56551–58, Mahor Birinji.

Pholidosis. Only in two specimens do the parietals meet behind the interparietals. Scale rows: in the specimens from Iraq, 37 in six specimens, 36 in three, 35 in one, and 34 in one; in the specimens from Iran, 34 in four specimens, 35 in two, 36 in one, and 37 in one.

Measurements. Largest (and apparently fully grown) specimens from Iraq—Snout-vent: 70–81 mm. Largest specimens from Iran—Snout-vent: 76–84 mm.

Coloration. A pair of broad, brown, lateral bands. Between these, four narrow, blackish, interrupted dorsal stripes.

Mabuya macularia Blyth

Euprepes sebae Duméril and Bibron (in part), 1839, Erpétol. Gén., 5: 692.
Mabuya macularia, Boulenger, 1887, Cat. Lizards Brit. Mus., 3: 182.

Material examined. WEST PAKISTAN (1): MCZ 54446, Tatta, Sind.

Pholidosis. Twenty-eight scale rows, dorsals with seven keels. Sixteen lamellae under 4th toe. The specimen differs from the description by Boulenger (1887) in having the frontal clearly longer than the combined lengths of frontoparietal and interparietal, and in having a fifth small (doubtful) supraocular. It is hard to assign the single preserved specimen to one of the five forms distinguished by Smith (1935).

Measurements. Snout-vent: 61 mm.

Mabuya vittata Olivier

Scincus vittatus Olivier, 1804, Voy. Emp. Othoman, 3: 103 (sands of Rosetta).
Mabuya vittata: Wettstein, 1928, Sitzungsber. Akad. Wiss. Wien, Math.-Naturw. Kl., Abt. 1, 137 (10): 783.

Material examined. IRAQ (6): MCZ 56538, 56544, 56547, Kish area; MCZ 56561–63, Havdian, at foot of Jebel Baradost near Ruwanduz.

Pholidosis. Thirty-one scale rows in three specimens, 32 in two, and 30 in one. MCZ 56563 shows an especially sharp treble keeling of the dorsal scales.

Measurements. Kish area—Snout-vent: 60–68 mm. Havdian—Snout-vent: 80–87 mm.

Coloration. All six specimens have two broad, dark brown, dorsal stripes and a lateral pair of broad dark stripes. In specimens from the Kish area, the middorsal light-colored (greyish) band is approximately twice as wide as each lateral light-colored band. The dark bands are framed in black, especially towards the middorsal light band, and at the lateral (lower) margin of the lateral dark pair. In specimens from Havdian, the dorsal pair of dark bands lacks the medial black seam, showing instead a dark mottled pattern which may or may not be emphasized towards the middorsal light band. Irregular mottling occurs also on the lateral dark stripes.

Ophiomorus tridactylus Blyth

Sphenocephalus tridactylus Blyth, 1855, J. Asiat. Soc. Bengal, 22: 654 (Afghanistan).
Ophiomorus tridactylus: Boulenger, 1887, Cat. Lizards Brit. Mus., 3: 394.

Material examined. WEST PAKISTAN (1): MCZ 54445, Saradoo.

Pholidosis. Twenty-two scale rows.

Measurements. Snout-vent: 91 mm.

Scincus conirostris Blanford

Scincus conirostris Blanford, 1881, Proc. Zool. Soc. London, 1881: 677, fig. 1 (Tangyak, 7 mi. S of Bushire).

Material examined. SAUDI ARABIA (1): MCZ 56564, between Al-Gaisumah and Turaif on Tapline.

Pholidosis. Twenty-six scale rows. Prefrontal well separated from rostral by sagittally continguous supranasals.

Measurements. Snout-vent: 59 mm.

Coloration. Uniformly colored, without transverse bars (young *S. officinalis* of equal size are similarly colored; the bars develop later in life).

Remarks. This form is considered a subspecies of *S. scincus* by Khalaf (1959: 49), who does not state his reasons.

Chalcides ocellatus ocellatus Forskål

Lacerta ocellata Forskål, 1775, Descr. Anim., p. 13 (Egypt).

Chalcides ocellatus forma *typica*, Boulenger, 1890, Ann. Mag. Nat. Hist., 51: 444.

Material examined. TRUCIAL OMAN COAST (3): MCZ 56534–36, Sharjah.

Pholidosis. All three specimens have 28 scale rows at midbody.

Measurements. Snout-vent: 97, 73, and 90 mm.

Coloration. These specimens seem to be much darker than animals from Israel. Each of the upper and lower labials, beginning with the second, has a broad black rim on its dorsal, ventral, and caudal borders, so that the lips bear a kind of zebra striping. In some regions, especially on the sides of the neck, the black mottling dominates over the paler interstices. In each of the numerous dorsal ocelli, the white center is reduced to a narrow streak (narrower than in specimens from Israel, in general). The dorsal ocelli tend to become confluent laterally (especially so in MCZ 56536: the crossbar-like fusions are irregular on its back and flanks, but very regular in the dorsopectoral area). On the tail (behind its base) the ocellated scales form regular transverse bands, each two separated by a double ring of pale scales.

ORDER AMPHISBAENIA

Family Trogonophidae

Diplometopon zarudnyi Nikolski

Diplometopon zarudnyi Nikolski, 1907, Ann. Zool. Mus. Acad. Sci. St. Petersburg, 10: 277 (Nasrie, Arabistan, Iran).

Material examined. SAUDI ARABIA (2): MCZ 56537, 57176, along Trans-Arabian Pipeline (Tapline) between Al-Gaisumah and Turaif.

Pholidosis. The postfrontal (Gans, 1960: 139; = frontal, Haas, 1957: 72) is almost completely bisected by the median groove in MCZ 56537, but not in MCZ 57176, in which the groove divides only the posterior two thirds of that shield. Of the two preoculars (?) the lower (loreal?) is much more elongated, and the upper consequently much larger, than in the specimens depicted by Haas (1957: 71, fig. 8) and Gans (1960: 140, fig. 3). Body annuli (Gans, 1961: 6) of MCZ 56537 (the other specimen being badly damaged), 178; postanal annuli, 20; anals, 8.

Measurements (MCZ 56537). Snout-vent: 149 mm. Tail: 14 mm. (The specimen is strongly contorted.)

Coloration. A pinkish brown, speckled dorsally with blackish brown dots; similar to specimen depicted by Gans (1960: 45, fig. 3), but the dark dots extend on the tail to the penultimate annulus.

ORDER OPHIDIA

Family Typhlopidae

Typhlops cf. *vermicularis* Merrem

Typhlops vermicularis Merrem, 1820, Tent. Syst. Amphib., p. 158 (Greek Islands—Mertens and Müller, 1928).

Material examined. IRAN (1): HF-30, Mazuo.

Measnrements. Total length, about 200 mm.

Family Boidae

Eryx jaculus sspp.

Anguis jaculus Linnaeus, 1758, Syst. Nat., ed. 10, 1: 228 (Egypt).
Eryx jaculus, Daudin, 1803, Hist. Nat. Rept., 7: 257.

Material examined. IRAQ (7): MCZ 56870–71, Lake Habbaniya; MCZ 56872–75, Kish area; MCZ 58874, Abu Ghraib, W of Baghdad. IRAN (1): MCZ 56876, Mahor Birinji.

Pholidosis. Interorbital scales (from eye to eye): 5–6 (mean, 5.6). Scales surrounding eye: 8–11 (mean, 9.6). Upper labials: 9–11 (mean, 9.8). Scale rows: 41–52 (mean, 48.3). Ventrals: 180–194 (mean, 187.7). Subcaudals: 22–32 (mean, 27.6). Regarding the last three characters, the specimen from Iran represents the short-tailed extreme of the variation: ventrals, 192; subcaudals, 22 (it has 51 scale rows).

Measurements. The snakes are rather contorted and difficult to measure accurately. The largest (MCZ 56871 from Lake Habbaniya) measures at least 480 mm snout-vent, 49 mm tail. The specimen from Iran (MCZ 56876) also measures 480 mm snout-vent; its tail is 46 mm.

Coloration. All specimens from Iraq have brown backs, with light, irregular blotches, some confluent to form an irregular zig-zag band, some more like cross-bands. The brown margins of the light areas are spotted here and there with darker brown. Flanks are also spotted with the darker brown. In the specimen from Iran the back is best described as being of a light (cream) color, with a median series of very irregular brown blotches, some anteriorly) confluent. On each side there is a dorsolateral band of still darker brown, of irregular width, sometimes interrupted. Lateral (and ventral) to this, the light ground color is mottled in two shades of brown.

Remarks. We find it impossible to arrive at a satisfactory determination of this material on the subspecific level.

Family Colubridae

Natrix tessellata tessellata (Laurenti)

Coronella tessellata Laurenti, 1768, Synops. Rept., 87 ("in Japidia, vulgo Cars").
Natrix tessellata: Bonaparte, 1834, Iconogr. Faun. Ital., Fasc. 2, 11: Plate, fig. 2.
Natrix tessellata tessellata: Sochurek, 1956, Burgenl. Heimatbl., 18: 89.

Material examined. IRAQ (1): MCZ 57014, Kish area. IRAN (2): MCZ 57015, Dorud; MCZ 58873, 4 mi. W of Gotwand. WITHOUT DATA (4): HF-79, probably Kish area, Hilla, Iraq.

Pholidosis. Specimens with data: scale rows (at midbody), 19; 19; 21. Ventrals, 168; 177; 169. Subcaudals, 70; 59; 65.

Measurements (largest specimen [MCZ 57015]). Snout-vent: at least 590 mm. Tail: 134 mm.

Coloration. Two specimens represent extremes of the normally very variable ventral pattern. In MCZ 57014 the black areas are particularly restricted; in MCZ 57015 the black color of the posterior abdomen is continued anteriorly (for half the length of the animal) as a median band, of which only the anterior ten ventrals are free (from about the 30th ventral backwards there is also an increasing amount of black mottling on both sides of the median band).

Coluber jugularis asianus (Boettger)

Zamenis viridiflavus var. *asiana* Boettger, 1880, Ber. Senckenb. Naturf. Ges., 1879–80: 151.
Coluber jugularis asianus: Müller and Wettstein, 1933, Sitzungsber. Akad. Wiss. Wien Math.-Naturw. Kl., Abt. 1, 143: 142.

Material examined. IRAQ (3): MCZ 58869, ♀, 58870, ♂, Havdian, near Ruwanduz; MCZ 58871, ♂, Lake Habbaniya.

Pholidosis. Scale rows: 21. Ventrals: 198–208. Subcaudals: 106–109.

Measurements (Largest specimen [MCZ 58869]). Snout-vent: about 940 mm. Tail: about 335 mm.

Coloration. The specimens from Havdian are almost black dorsally; in MCZ 58869 many of the dorsal scales are speckled with

whitish, these light specks often forming a fine line along the middle of the scale (especially near the middle of the body); in MCZ 58870 a very delicate light line runs along each longitudinal series of scales (through the middle of each scale), this pattern increasing in distinctness towards the tail. In both specimens the ventral side is beige (with traces of pink) and heavily speckled with black, in a semi-regular pattern, leaving on every scute an unspeckled crossband close to (not bordering) its caudal margin. The specimen from Lake Habbaniya is brownish grey, and along each longitudinal row of dorsal scales there runs a band of lighter grey, occupying the median third of each scale, and not sharply delimited. Ventrally the black specks are mostly confined to both lateral thirds of each scute.

Remarks. According to Khalaf (1959: 75), this snake may reach a length of eight feet. The same, more or less, is true of the Israel population of *C. jugularis.* In comparison to specimens from Israel of equal length, our specimens from Iraq are rather thick bodied. Furthermore, such half-grown specimens from Israel would not have attained the uniform (black) adult coloration, but would, rather, show remnants of the juvenile pattern of darker and lighter spots. Conceivably the specimen from Lake Habbaniya, at least, also presents a relatively light juvenile coloration (Khalaf, 1959: 75).

Coluber ventromaculatus Gray

Coluber ventromaculatus Gray (and Hardwicke), 1834, Illus. Indian Zool., 2: pl. 89, fig. 1 (Bengal—Schmidt, 1939: 74).

Material examined. IRAQ (1): MCZ 58868, Kish area. WEST PAKISTAN (1): MCZ 54401, ♂, Tatta, in Sind, E of Karachi, 8 March 1955. WITHOUT DATA (1): HF-79, probably Kish area, Hilla, Iraq.

Pholidosis. Scale rows: 19. Ventrals: 203; 197; 187. Subcaudals: 99; 110; 88.

Measurements (largest specimen [MCZ 54401]). Snout-vent: about 480 mm. Tail: about 200 mm. The others are juveniles, about 260 and 295 mm snout-vent.

Coloration. The pattern of dark crossbands disappears at the level of the cloaca in the adult, but is continued throughout the tail as a series of vertebral spots, then dots in the two juveniles.

Remarks. According to Minton (1966: 121) this snake occurs over much of Southwestern Asia, including Israel. We would like to make use of this opportunity to state that we are aware of no snake specimens from Cisjordan referable to this species.

Coluber rhodorachis rhodorachis (Jan)

Zamenis rhodorachis Jan, 1865, *in* De Filippi, Viagg. Persia, p. 356 (Iran; restricted to Schiras [Shiraz], Central Persia—Kramer and Schnurrenberger, 1963: 501).

Coluber rhodorachis, Parker, 1931, Ann. Mag. Nat. Hist., (10) 8: 516.

Coluber rhodorachis rhodorachis, Khalaf, 1959, Reptiles of Iraq with some notes on the amphibians, Baghdad, pp. 75–76.

Material examined. IRAN (1): MCZ 58872, Mahor Birinji.

Pholidosis. Scale rows (at midbody): 19. Ventrals: 236. Subcaudals: 137.

Measurements. Snout-vent: about 675 mm. Tail: 280 mm.

Coloration. Anterior half of body with crossbands, posterior half uniform. The first third of the banded region is uniquely patterned, in that the dark crossbands are broader (covering the length of about one scale).

Remarks. The pattern is surprising, as the several specimens from southern Israel we have examined have dark crossbands that are narrower than the light interspaces, and this is also the pattern of a specimen from Karachi, West Pakistan, depicted by Minton (1966: pl. 25, fig. 1). Another specimen with *broad* dark crossbands has recently been collected at Petra, Jordan (Y. L. Werner, in MS).

Eirenis persica (John Anderson)

Cyclophis persicus Anderson, 1872, Proc. Zool. Soc. London, 1872: 392, fig. 8 (Bushire, Persia).

Eirenis persica, Stickel, 1951, Herpetologica, 7: 128.

Material examined. IRAN (3): HF-40, Shalgahi: HF-51(13) and HF-51(14), Mahor Birinji. (All in bad condition.)

Pholidosis. Loreal absent, one pre- and one postocular. Upper labial: 7 (but apparently 8/8 in HF-51(13)). Lower labials: 7. Scale rows: 15. Ventrals: (?)194–206. Subcaudals: 50–64.

Measurements (largest specimen [HF-40]). Snout-vent: 241 mm. Tail: 58 mm.

Coloration. One of the specimens from Mahor Birinji (14) has a barred pattern (= "Eirenis persica nigrofasciata Nik."); the other two have unicolored bodies. The latter have three blackish crossbands on the head—one through the supraoculars, one through the parietal, and one on the nape. In the barred specimen, the second and third crossbands are confluent. It has about 57 black half-rings on the body, and thirteen on the tail. Each is one to two scales broad, and the light (yellowish) intervals are three to four scales broad. The ventral side of all specimens is light, uniformly colored.

Remarks. The fact that both a barred and unicolored specimen have been collected at the same place (Mahor Birinji) supports Minton's (1966:129) suggestion that these patterns do not indicate geographic races. Thus a subspecific taxonomy of the species, based on the pattern only, appears invalid. Probably the two color patterns represent "phases" of the same population, as has also been suggested by Minton; but the possibility of their representing two sympatric (? sibling) species has not yet been conclusively ruled out.

Eirenis collaris (Ménétriés)

Coluber collaris Ménétriés, 1832, Cat. Rais. Obj. Zool. . . . Voy. Caucase . . . , p. 67 (Becheber-mak, near Caspian Sea).
Eirenis collaris, Jan, 1863, Arch. Zool. Anat. Fisiol., Genova, 2: 256.

Material examined. WITHOUT DATA (1): HF-79, probably Kish area, Iraq.

Pholidosis. Loreal: present. Preoculars: 2/1. Postoculars: 2/2. Upper labials: 7/7. Lower labials: 8/8. Scale rows: 15. Ventrals: 170. Subcaudals: 53.

Measurements. Snout-vent: 225 mm. Tail: 61 mm.

Coloration. Head mottled with black. A broad, black (very dark brown) crossband on the occiput reaches the sides of the throat, where it is pointed anteriorly. Body with delicate dark longitudinal lines running through the margins of the scales.

Eirenis coronella cf. *coronella* (Schlegel)

Calamaria coronella Schlegel, 1837, Physion. Serp., 2: 48 (Syria—Schmidt, 1939: 78).
Eirenis coronella coronella, Schmidt, 1939, Field Mus. Nat. Hist., Zool. Ser., 24: 78.

Material examined. IRAN (2): HF-40, ♂, Shalgahi. HF-49, juvenile, Mahor Birinji.

Pholidosis. Loreal present. Preocular: single. Postoculars: 2/2; 2/1. Upper labials: 7/7; 8/8. Lower labials: 6/6; 7/7. Temporals: 1+2/1+1; 1+1/1+1. Scale rows: 15; 15. Ventrals: ? (damaged); 140. Subcaudals: 43; 44.

Measurements (HF-49). Snout-vent: 148 mm. Tail: 37 mm. (HF-40 is too badly damaged to measure.)

Coloration. Back with brown crossbands (= half-rings), each about two scales broad, with the lighter intervals about three scales broad. A broad occipital crossband extends to the sides of the throat. Number of dark crossbands (HF-49) on body, 49; on tail, 15. Ventral side uniformly pale buff.

Rhynchocalamus sp.

Plate 20

Material examined. IRAN (1): MCZ 56877, Shalgahi.

Pholidosis. Nasal undivided. Loreal present, about twice the size of the preocular. Preocular and postocular single. The large, spatulate rostral nearly separates the internasals; it is as long (seen from above) as the combined sutures be-

tween the two internasals and between the two prefrontals. Upper labials: 7/7. Lower labials: (?) 8/8. Scale rows: 15. Ventrals: 219. Subcaudals: 62.

Measurements. Snout-vent: 138 mm. Tail: 28 mm.

Coloration. Pale yellowish beige, without any pattern except for a pair of brown patches on the neck. Each patch starts about three scales behind the pileus, is about eight scales long, and one to two scales broad (narrow anteriorly, broad posteriorly). There is also a microscopical brown patch at the upper anterior corner of each eye.

Remarks. This appears to be the specimen described by Reed and Marx (1959: 109–113) under *R. satunini* Nikolski, HF-40. It is true that the pholidosis of our specimen agrees with that of *R. satunini*, which these authors separate from *R. melanocephalus* Jan, and in particular with that of specimen FMNH 74605, from Jarmo in northern Iraq. However, the difference in pattern between our specimen and all *satunini* specimens recorded so far from Anatolia, Armenia, and northern Iraq is striking. It is hard to accept Reed's and Marx's interpretation of the pattern of the Shalgahi specimen as being that of a juvenile, since normally when a juvenile pattern changes into a different adult pattern a process of reduction is involved—not one of expansion, as would be the case here. We feel it would be premature to apply specific or subspecific determination to the single juvenile specimen before us, which apparently is the only specimen of the genus so far reported from Iran. It is evidently closely allied to *R. satunini*. Among the Pakistanian forms, *Oligodon taeniolatus* (Jerdon) is the most similar in pholidosis to the Shalgahi specimen, yet has a divided nasal and higher numbers of postoculars and temporals (at least within Pakistan, if not within India—Minton, 1966: 133).

Psammophis cf. *schokari* Forskål

Coluber schokari Forskål, 1775, Descr. Anim., p. 14 (Yemen, S. Arabia).
Psammophis schokari, Boulenger, 1896, Cat. Snakes Brit. Mus., 3: 157.

Material examined. IRAN (1): HF-49 ("10"), Mahor Birinji.

Pholidosis. Scale-rows: 17. Ventrals: 179. Subcaudals: 125.

Measurements. Snout-vent: about 400 mm. Tail: 197 mm.

Coloration. A pattern of four dark brown longitudinal bands, which does not include the pileus; latter adorned with complex anchor-like pattern. The two median bands are separated from each other by less than the breadth of a scale. On each of the four dark bands the margins are accentuated by a row of darker dashes. There is a pair of ventrolateral delicate dark lines.

Remarks. The badly damaged head introduces an element of doubt into the identification of this specimen.

Psammophis leithi Günther

Psammophis leithi Günther, 1869, Proc. Zool. Soc. London, 1869: 505, pl. 39 (Sind).

Material examined. WEST PAKISTAN (1): MCZ 54406, juvenile, Big Kapoto, 10 mi. S of Kalat, Baluchistan, 1955.

Pholidosis. Scale rows: 17. Ventrals: 178. Subcaudals: 105.

Measurements. Snout-vent: about 300 mm. Tail: about 130 mm.

Coloration. Back with two pairs of dark bands, the median pair a nearly uniform blackish brown; each lateral band is of a somewhat lighter shade, with darker margins (same color as median bands). The lateral bands extend forward to the eye, and are represented in a somewhat modified manner on the snout. The median pair is continued forward, on either side of the pileus, to the nostril. Along the middle of the pileus, from the suture between prefrontals and frontal to the end of the parietals, there runs a fifth brown band.

This pattern apparently agrees with that described by Minton (1966: 141) of *P. leithi* from West Pakistan, but differs somewhat from that depicted by Smith (1943: 366) of the British Museum specimen BM 91.9.1.5.

Family Elapidae

Walterinnesia aegyptia Lataste Plate 21

Walterinnesia aegyptia Lataste, 1887, Le Naturaliste, 1887: 411 (Egypt).

Material examined. IRAN (1): MCZ 56878, Mahor Birinji.

Pholidosis. Scale rows: 23. Ventrals: 193. Subcaudals: 44. On the right side there are two preoculars, both touching the nasal.

Measurements. Snout-vent: about 355 mm. Tail: 47 mm.

Coloration. This specimen, evidently a juvenile, is striking in having the typical dark color (in this case, a very dark violet-brown) interrupted by 26 fairly regular, narrow, pale crossbands (pinkish brown). Each pale saddle is no broader middorsally than the length of one or one and a half scales, but each broadens ventrolaterally to a maximum breadth equalling the length of three scales. Ventrolaterally the light saddles are separated from the similarly light ventrals by two rows of normal dark scales. Middorsally the dark areas between succeeding light saddles occupy as much as six to seven scales. In the nuchal region there is an indication of a ventrolateral pale connection from the third pale saddle towards the head, indicating a modified nuchal pattern. The light crossbands stop a short distance before the vent, but a few light spots are scattered on the anterior third of the tail.

Remarks. S. C. Anderson (1963: 470–471) mentions three specimens from the very same area and refers to a fourth, juvenile, specimen, in the collection of the hospital at Masjid-i-Suleiman, as having "very narrow light crossbands." We are acquainted with juveniles of *Walterinnesia aegyptia* from Israel, of similar and smaller sizes. These have the typical uniform blackish color of the adults. It is noteworthy that the place of origin of the cross-banded juveniles coincides with the type localities for *Naja morgani* Mocquard 1905 (= *Atractaspis wilsoni* Wall 1908—Marx, 1953), as S. C. Anderson (1963: 470) pointed out. Perhaps, after all, *Naja morgani* and *Walterinnesia aegyptia* are not quite the same thing. A reinvestigation of this problem should take into account a greater number of characters, including the color pattern.

Family Viperidae

Vipera lebetina cf. *euphratica* (Martin)

Vipera euphratica Martin, 1838, Proc. Zool. Soc. London, 1838: 82 (Euphrates Valley).

Vipera lebetina euphratica, Schmidt, 1939, Field Mus. Nat. Hist., Zool. Ser., 24 (7): 87.

Material examined. IRAQ (1): MCZ 58875, ♂, Havdian, near Ruwanduz. WITHOUT DATA (1): HF-79, ♂, probably Kish.

Pholidosis. Upper labials: 11/12; 11/10. Lower labials: 13/13; 12/13. (The labial counts for the first specimen are somewhat doubtful owing to the badly damaged head.) Scale rows: 25; 27. Ventrals: 170; 173. Subcaudals: 45; 46.

Measurements. MCZ 58875—Snout-vent: 630 mm. Tail: 93 mm. HF-79—Snout-vent: 265 mm. Tail: 43 mm.

Coloration. Back with traces of dark crossbands, which even in the juvenile are not distinct enough to be counted. Darker crossbands on each flank (ventrolaterally) alternate with these. The ventral side is stippled with brownish grey; part of the stippling of each scute is concentrated into a few roundish spots. The lateralmost of these are darkest, and confluent with the ventrolateral crossbands. The most distinct markings on the head are a couple of blackish brown spots on either lower lip.

Remarks. Schmidt (1939: 87) reports on a specimen measuring 1270 mm from snout to vent (tail, 150 mm), from Balad Sinjar, northwestern Iraq.

Cerastes cerastes (Linnaeus)

Coluber cerastes Linnaeus, 1758, Syst. Nat., p. 271 ("Oriente"—see remarks below).
Cerastes cornutus, Boulenger, 1896, Cat. Snakes Brit. Mus., 3: 502.
Cerastes cerastes, Anderson, 1899, K. Svenska Vetensk-Akad. Handl., Stockholm, Bihang, (4) 24 (6): 29.

Material examined. SAUDI ARABIA (1): Badanah on Tapline, without number, head only.

Pholidosis. Rows of scales between eye and upper labials (counted diagonally): 5/6. Number of scales surrounding eye: 15/16. Horns well developed, as long (base included) as the distance from snout to eye; each surrounded by five basal scales. Upper labials, 15 15; lower labials, 15 15.

Remarks. Haas (1957: 82–83) reports on 23 specimens from Saudi Arabia, only five of which were horned. In Sinai, too, there occur both horned and hornless specimens (Flower, 1933: 831). However, in Israel (in the Wadi Arava [Wadi Araba]), only hornless specimens have been found so far (personal observation). Therefore, Schmidt's (1939: 88) restriction of the type locality to "southern Judaea," appears to be in conflict with the fact that the original description was of a horned snake (Linnaeus, 1766: 376). In fact, Hasselquist (1766: 221) says expressly, "Coluber cerastes. The horned Viper. It is a native of Egypt." Hence there is every reason to accept Flower's (1933: 830) restriction of the type locality to Egypt (Kramer and Schnurrenberger, 1963: 539).

Echis carinatus (Schneider)

Pseudoboa carinata Schneider, 1801, Hist. Amphib., 2: 285 (India: Arni, near Madras—Minton, 1966: 159).
Echis carinatus, Wagler, 1830, Natürliches System der Amphibien, etc., Munich, p. 177.

Material examined. WEST PAKISTAN (1): MCZ 54405, Tatta, in Sind, E of Karachi.

Pholidosis. Scale rows: 29. Ventrals: 170. Subcaudals: 34.

Measurements. Snout-vent: 523 mm. Tail: 54 mm.

Coloration. The pattern is typical (Minton, 1966: 160, pl. 36, fig. 1). There are 36 white vertebral spots on the body and 8 small ones on the tail.

Remarks. Constable (1949) divided this species into two subspecies, but Minton (1966: 160) showed that this arrangement is not acceptable without further study.

DISCUSSION

General Biogeography of Southwestern Asia. The entire area from which the present material originates (excepting, perhaps, the Trucial Oman Coast) was included by Wallace (1876) in his Mediterranean Sub-Region of the Palaearctic Region. Wallace's subdivision of the Palaearctic, like the rest of his zoogeography, has been enjoying general acceptance (thus Bartholomew, *et al.*, 1911; Swan and Leviton, 1962), although the justification of a separate Mediterranean sub-region, in particular, has been questioned by zoogeographers. According to Beaufort (1951: 41), this is only a "transition region," which is "often considered . . . distinct," and Darlington (1957: 442) does not consider it "worth formal recognition, although 'Mediterranean' is a useful descriptive term for some distributions."

A school of Near East biogeographers, with which most herpetologists are not familiar, maintains that the vagueness of Wallace's Mediterranean Sub-Region is due not to his having split off an unreal unit, but to his having lumped together three territories that are quite different in general ecology and animal life. These are termed the Mediterranean (*sensu stricto*), Irano-Turanian, and Saharo-Sindian subregions (or regions, or territories). Together they occupy a somewhat wider area than the Mediterranean Sub-Region (*sensu lato*) of Wallace (Fig. 13). This arrangement, based on the work of Grisebach (1872), has been elaborated by the botanist Eig (1831) with particular reference to

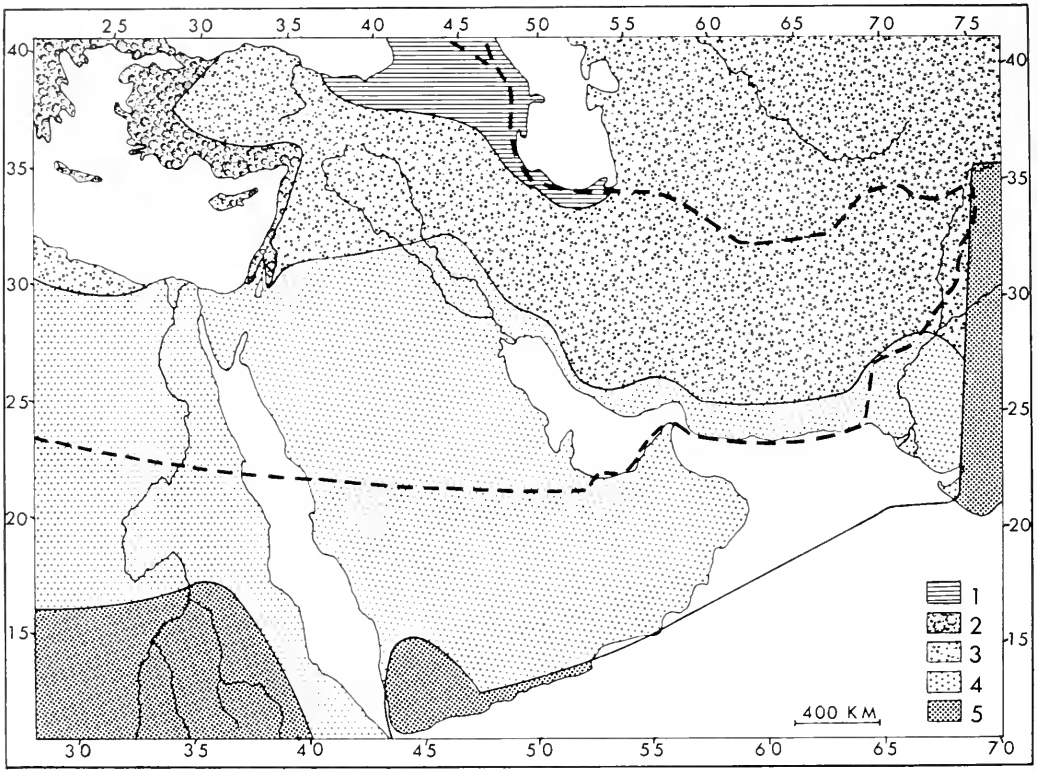

Figure 13. Sketch map of Southwestern Asia (with adjacent areas of Europe and Africa). The heavy interrupted line represents Wallace's (1876) boundary of the Mediterranean Sub-Region. Shaded areas represent zoogeographical regions after Bodenheimer (1956).

(1–4) Sub-Regions of the Palaearctic region: (1) Euro-Siberian Colchis Province; (2) Mediterranean; (3) Irano-Turanian; (4) Saharo-Sindian. (5) Sub-Regions of the Palaeotropic Region.

Palestine, and its basic concepts are accepted by contemporary Israeli botanists (thus Zohary, 1955; Zohary and Feinbrun-Dothan, 1966). Among zoologists, Bodenheimer (1935, 1937, 1953, and 1956) has been its chief advocate.

As Figure 13 shows, according to this arrangement, the area dealt with in this paper is divided between the Irano-Turanian and the Saharo-Sindian sub-regions. It must, of course, be realized that in nature there are usually no sharp boundaries between adjacent zoogeographical regions or sub-regions, but, rather, very broad zones of overlap.

In one respect, Bodenheimer's (Eig's) arrangement is a revision to Sclater's (1858) original proposal. In Africa and Southwestern Asia, Bodenheimer's line separating the Mediterranean and Irano-Turanian sub-regions, on the one hand, from the Saharo-Sindian Sub-Region, on the other, nearly coincides with Sclater's border between the Palearctic Region, on the one hand, and the Ethiopian and Indian regions, on the other (Bartholomew, *et al.*, 1911: pl. 2). As a matter of fact, in Southwestern Asia and North Africa, at least, Bodenheimer's map is in much better agreement with recent maps of soils, rainfall, and vegetation (e.g., Oxford Univ. Press, 1960) than is Wallace's map.

We shall not argue here the merits of either biogeographical scheme; our observations show only too well that the time is not yet ripe for a synthetic discussion of the herpetofauna of Southwestern Asia. Too many of the species are insufficiently known taxonomically, to say nothing of their biology, ecology, or exact distribution, which are almost unknown. Thus the herpetological material in itself can so far contribute little to zoogeographical discussions. Having briefly mentioned the two principal approaches to the biogeography of Southwestern Asia, we shall now merely present a list of the species reported here from each area.

Regional species lists. These lists are confined to material reported in the present paper. Specimens without data are excluded.

Syria (All localities are within the range of 250–1000 m above sea level).

Acanthodactylus cf. *tristrami orientalis* Angel
A. robustus F. Werner
A. grandis Boulenger
Eremias brevirostris brevirostis (Blanford)

Arabia (No further data).
Stenodactylus slevini Haas
Bunopus tuberculatus Blanford
Cerastes cerastes (Linnaeus)

Saudi Arabia: Along the Trans-Arabian Pipeline (Tapline) (including Turaif and Al-Gaisumah).
Agama cf. *persica* Blanford
A. persica fieldi subsp. nov.
A. pallida Reuss
Uromastix microlepis Blanford
Acanthodactylus boskianus asper (Audouin)
Eremias guttulata guttulata (Lichtenstein)
E. olivieri ssp.
E. brevirostris cf. *brevirostris* (Blanford)
Scincus conirostris Blanford
Diplometopon zarudnyi Nikolski

Arabian Peninsula and Bahrain Island. (including Dhahran, Al-Uqair, and Bahrain).
Bunopus blanfordii Strauch

Arabian Peninsula: Trucial Oman Coast (including Sharjah).
Hemidactylus flaviviridis Rüppell
Cyrtodactylus scaber (Heyden)
Pristurus cf. *rupestris* Blanford
Phrynocephalus cf. *maculatus* Anderson
Chalcides ocellatus ocellatus Forskål

Iraq: Slopes of the Kurdistan Mountains (including Haydian near Ruwanduz).
Lacerta trilineata media (Lantz and Cyrén)
L. cf. *strigata* Eichwald
Mabuya vittata Olivier
Coluber jugularis asianus Böttger
Vipera lebetina cf. *euphratica* (Martin)

Iraq: Qaara Depression North of Rutba (including IPC Station H-2; elevations between 250–1000 m).
Agama pallida Reuss
Eremias guttulata guttulata (Lichtenstein)
E. brevirostris brevirostris (Blanford)

Iraq: Euphrates Valley (including Abu Ghraib, Haditha, Lake Habbaniya, IPC Station K-3, IPC Station T-1; elevations between 0–500 m above sea level).
Bunopus tuberculatus Blanford
Ptyodactylus hasselquistii ssp.
Agama pallida Reuss
Acanthodactylus boskianus asper (Audouin)
A. scutellatus hardyi Haas
A. tristrami iracensis Schmidt
Eremias guttulata guttulata (Lichtenstein)
E. brevirostris brevirostris (Blanford)
Mabuya aurata septemtaeniata Reuss
M. vittata Olivier
Eryx jaculus ssp.
Natrix tessellata tessellata (Laurenti)
Coluber ventromaculatus Gray

Iran: Luristan Mountains (including Dorud, Mazuo, and Zagheh; all above 1000 m).
Phyllodactylus elisae (F. Werner)
Ophisops elegans cf. *elegans* Ménétriés

Typhlops cf. *vermicularis* Merrem
Natrix tessellata tessellata (Laurenti)

IRAN: HESHOM PLAIN (including Dizful, Gotwand, Mahor Birinji, and Shalgahi; all between 0–500 m above sea level).
Bunopus tuberculatus Blanford
Cyrtodactylus scaber (Heyden)
Agama agilis ssp.
A. nupta nupta De Filippi
Uromastix loricatus Blanford
Ophisops elegans cf. *elegans* Ménétriés
O. elegans ssp.
Eremias guttulata watsonana Stoliczka
E. brevirostris fieldi subsp. nov.
Mabuya aurata septemtaeniata Reuss
Eryx jaculus ssp.
Natrix tessellata tessellata (Laurenti)
Coluber rhodorachis rhodorachis (Jan)
Eirenis persica J. Anderson
E. coronella cf. *coronella* (Schlegel)
Rhynchocalamus sp.
Psammophis cf. *schokari* Forskål
Walterinnesia aegyptia Lataste

WEST PAKISTAN (mainly Baluchistan).
Hemidactylus flaviviridis Rüppell
Calotes versicolor (Daudin)
Agama agilis agilis ssp.
A. melanura Blyth
A. caucasica ssp.
Phrynocephalus scutellatus (Olivier)
Acanthodactylus cantoris blanfordi Boulenger
A. micropholis Blanford
Eremias guttulata watsonana Stoliczka
E. brevirostris brevirostris (Blanford)
Eumeces zarudnyi Nikolski
Mabuya macularia Blyth
Ophiomorus tridactylus Blyth
Coluber ventromaculatus Gray
Psammophis leithi Günther
Echis carinatus (Schneider)

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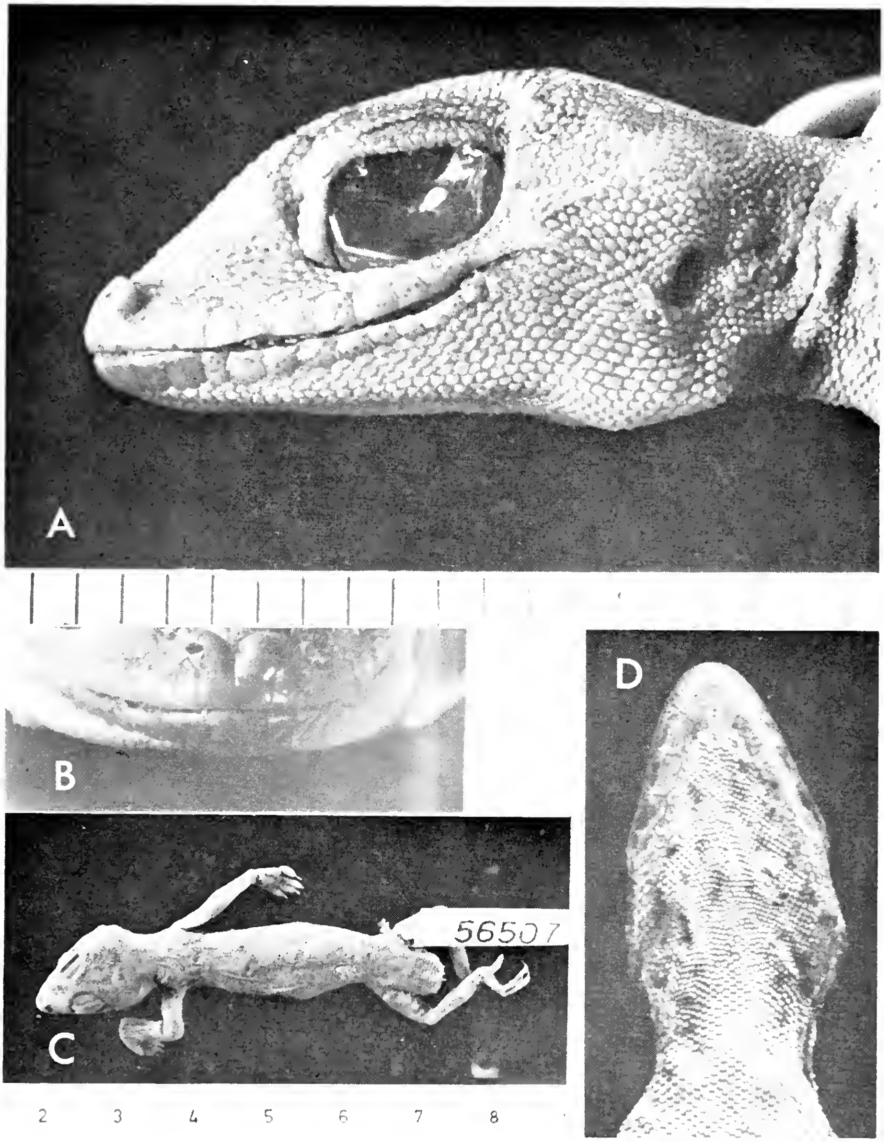


Plate 1. A–C, *Stenodactylus slevini*, MCZ 56507, ♂.
A, Head, lateral view.
B, Snout, anterior view.
C, Whole specimen, dorsal view.
D, *Pristurus* cf. *rupestris*, MCZ 56518, throat.
Scales: A, B, and D, at the same magnification, mm; C, cm and mm.

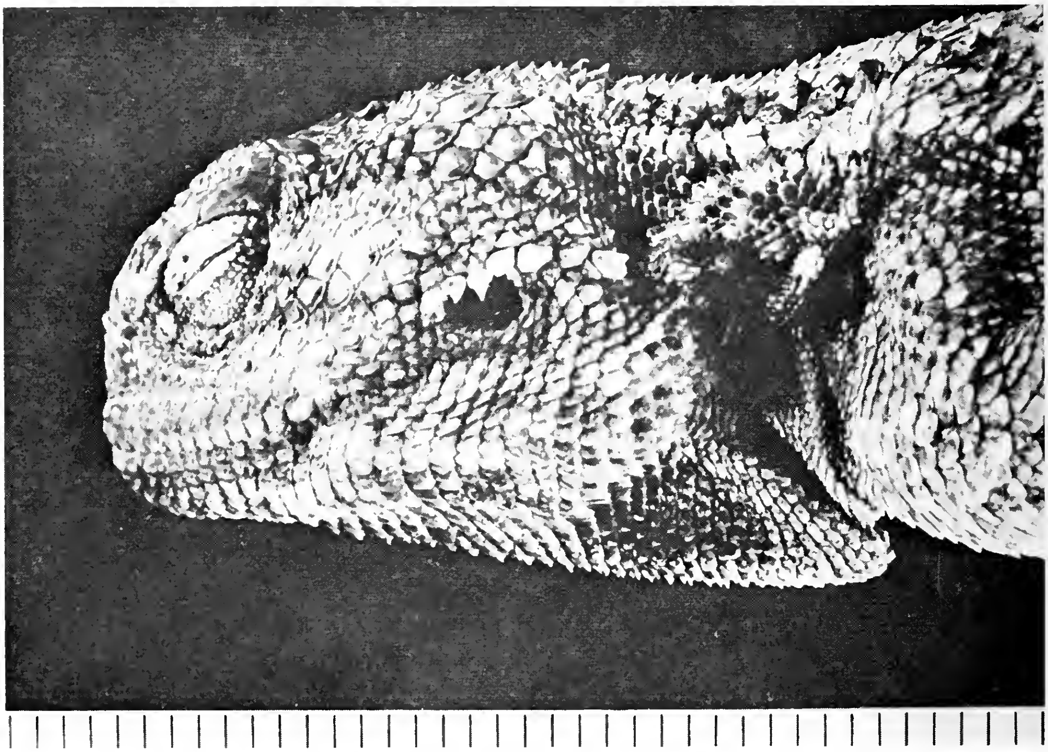


Plate 2. *Agama persica fieldi* subspec. nov., MCZ 56866, ♂, type. Head, lateral view. Scale: mm.

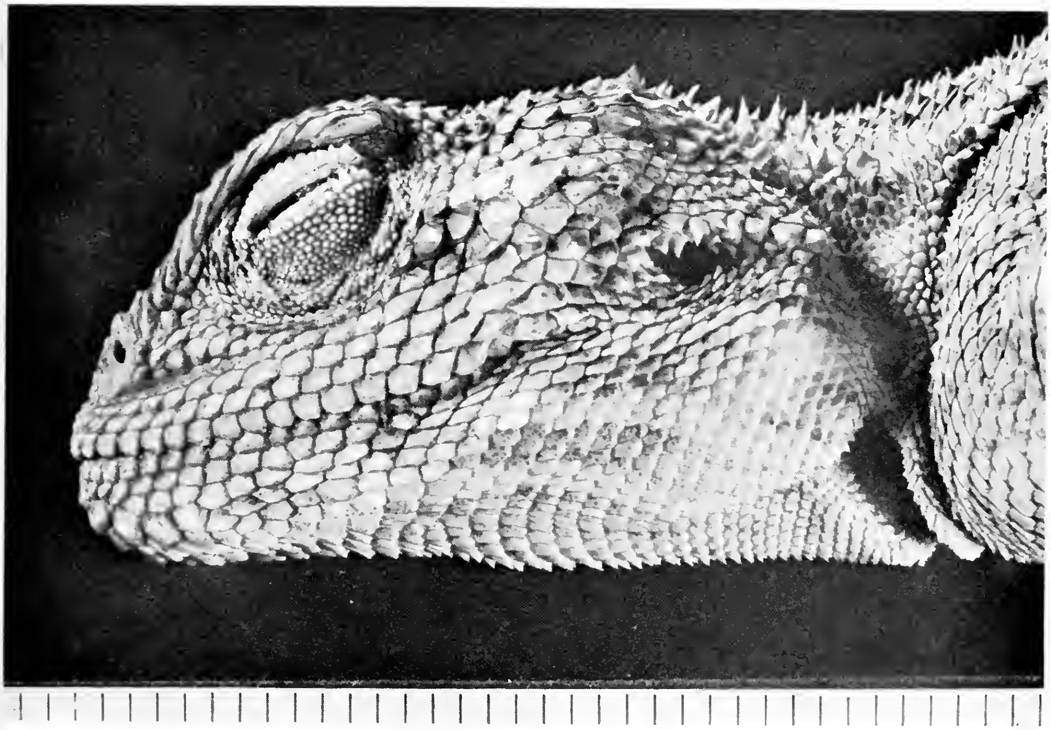
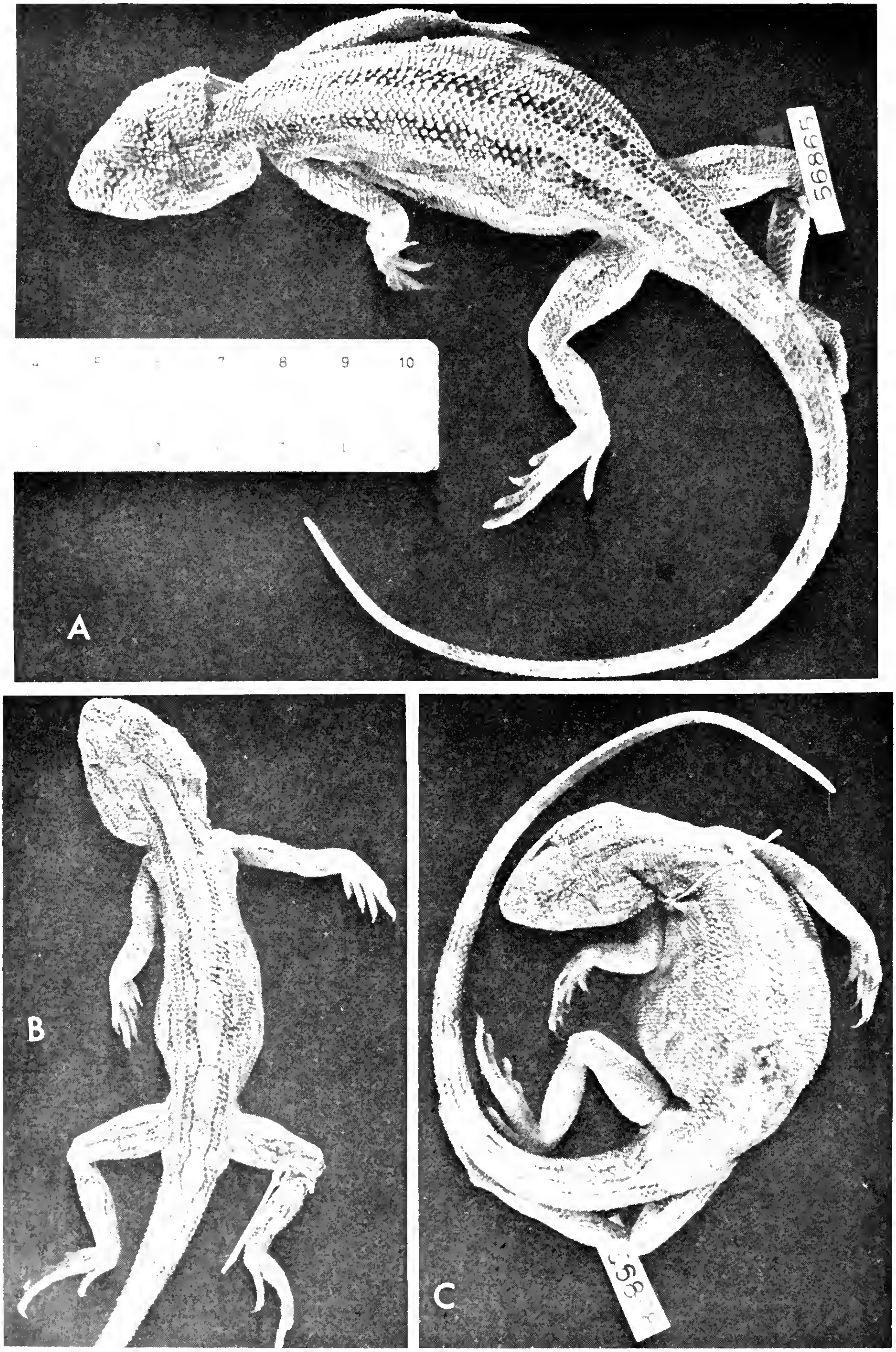


Plate 3. *Agama persica fieldi* subspec. nov., MCZ 56865, ♀ paratype. Head, lateral view. Scale: mm.


56866

Plate 4. *Agama persica fieldi* subspec. nov., MCZ 56866, ♂, type. Right, dorsal view; Left, ventral view. Scale: cm and mm.


56865
8 9 10
A
B
C

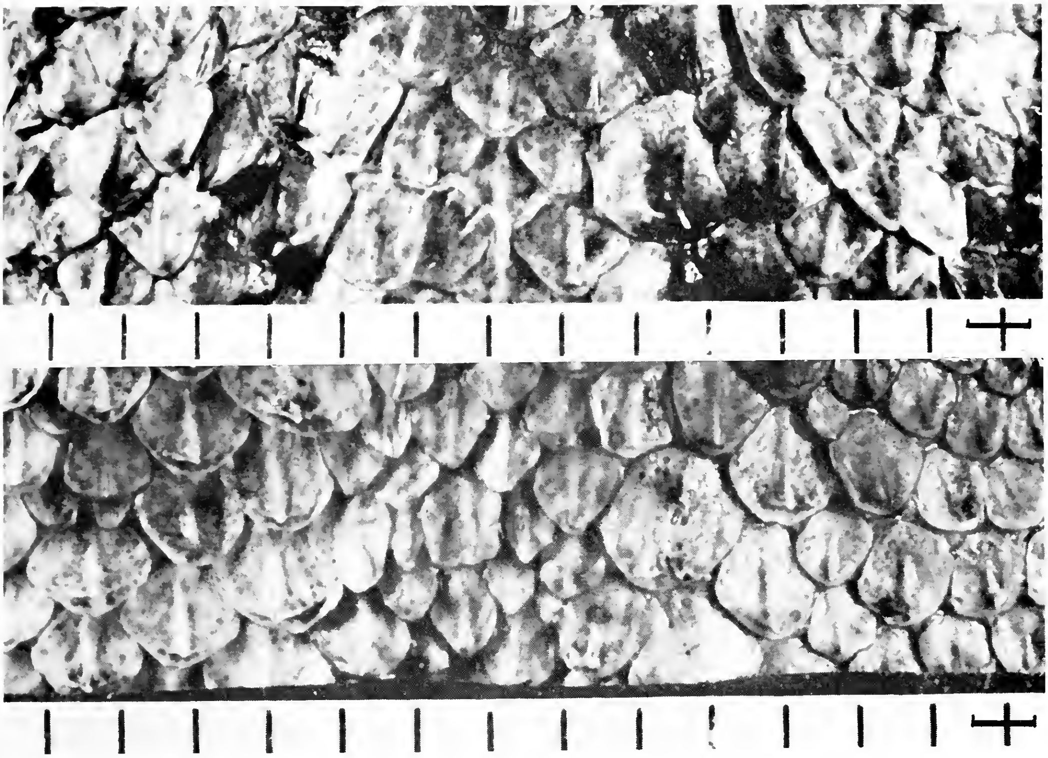


Plate 6. *Agama persica fieldi* subspec. nov., middorsal scales of:
Above, MCZ 56866, ♂, type.
Below, MCZ 56858, ♀ of "other material."
Scale: mm. The horizontal scale bar (at the lower right) represents 1 per cent of the snout–vent length of the respective specimen.

←

Plate 5. *Agama persica fieldi* subspec. nov., dorsal views of:
A, MCZ 56865, ♀ paratype.
B, MCZ 56864, juvenile paratype.
C, MCZ 56858, ♀ described under "other material."
All at the same magnification. Scale: cm and mm.

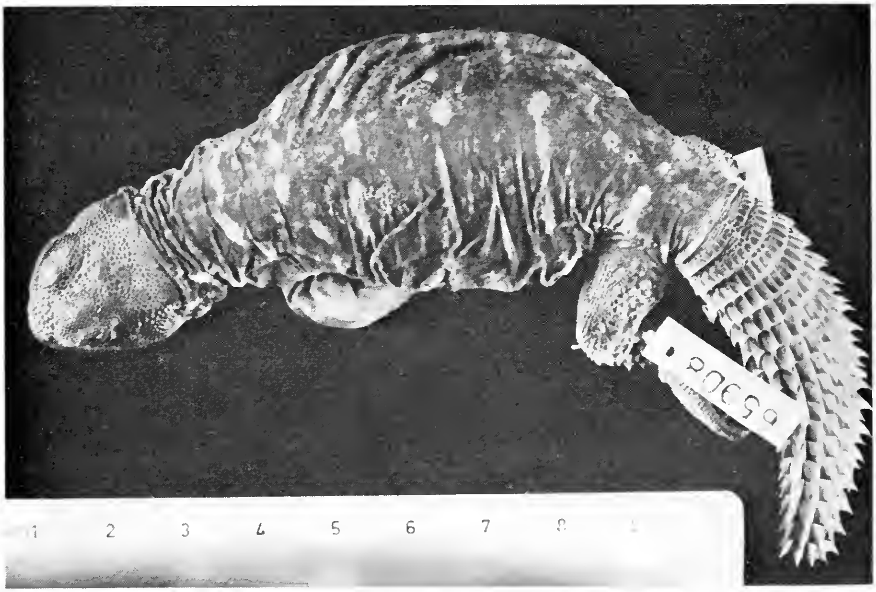
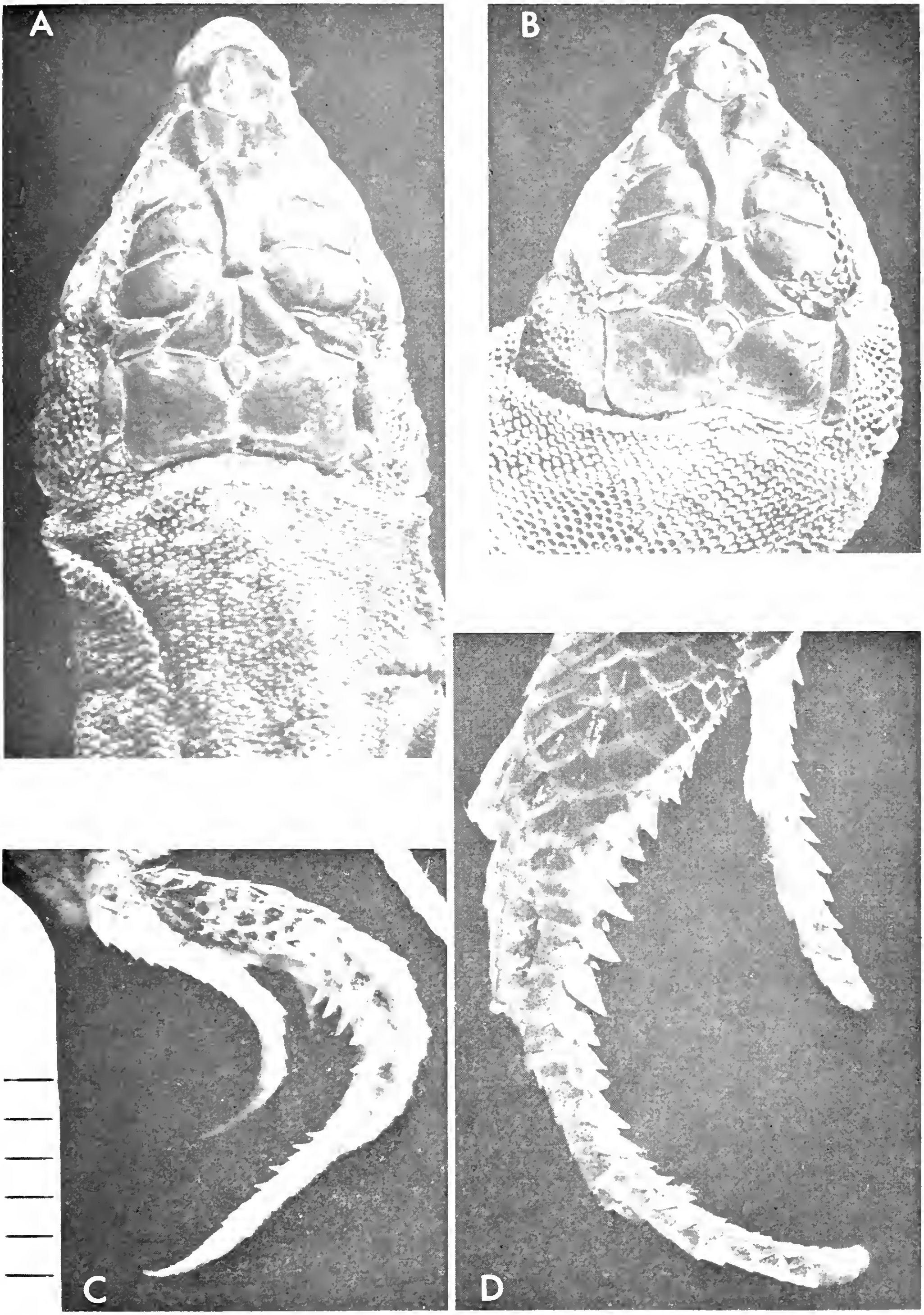


Plate 7. *Uromastix microlepis*, MCZ 56831 (FMNH 65908). Juvenile, dorsal view. Scale: cm and mm.

→

Plate 8. A–C, *Acanthodactylus scutellatus hardyi*.
A, MCZ 56652, head, dorsal view.
B, MCZ 56650, head, dorsal view.
C, MCZ 56652, right foot.
D, *Acanthodactylus boskianus asper*, MCZ 56643, left foot.
All at the same magnification. Scale: mm.


A
B
C
D

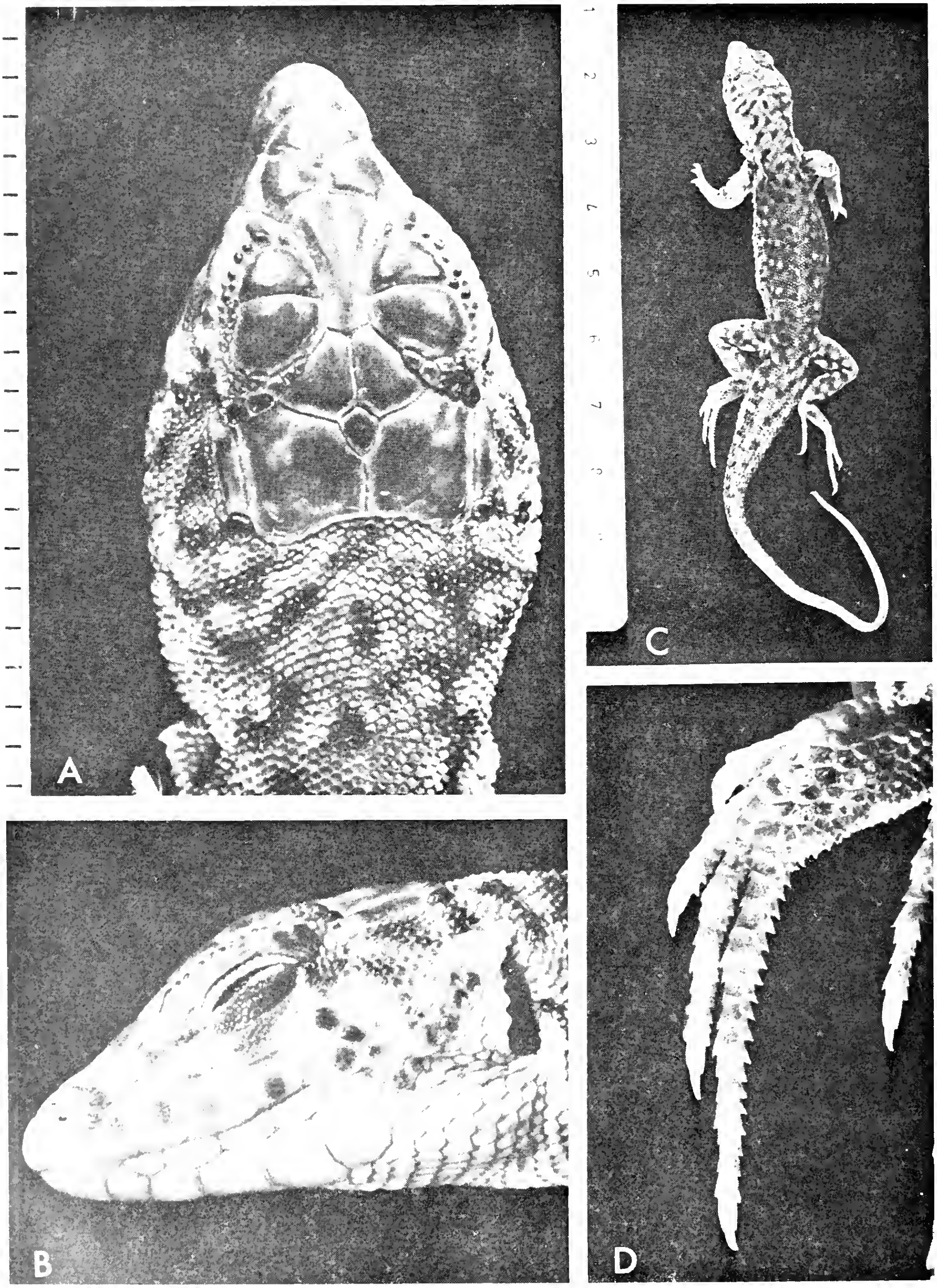

A
B
C
D

Plate 9. *Acanthodactylus tristrami iracensis*, MCZ 56654.
A, Head, dorsal view.
B, Head, lateral view.
C, Whole specimen, dorsal view.
D, Left foot.
Scales: A, B, and D, at the same magnification, mm; C, cm and mm.

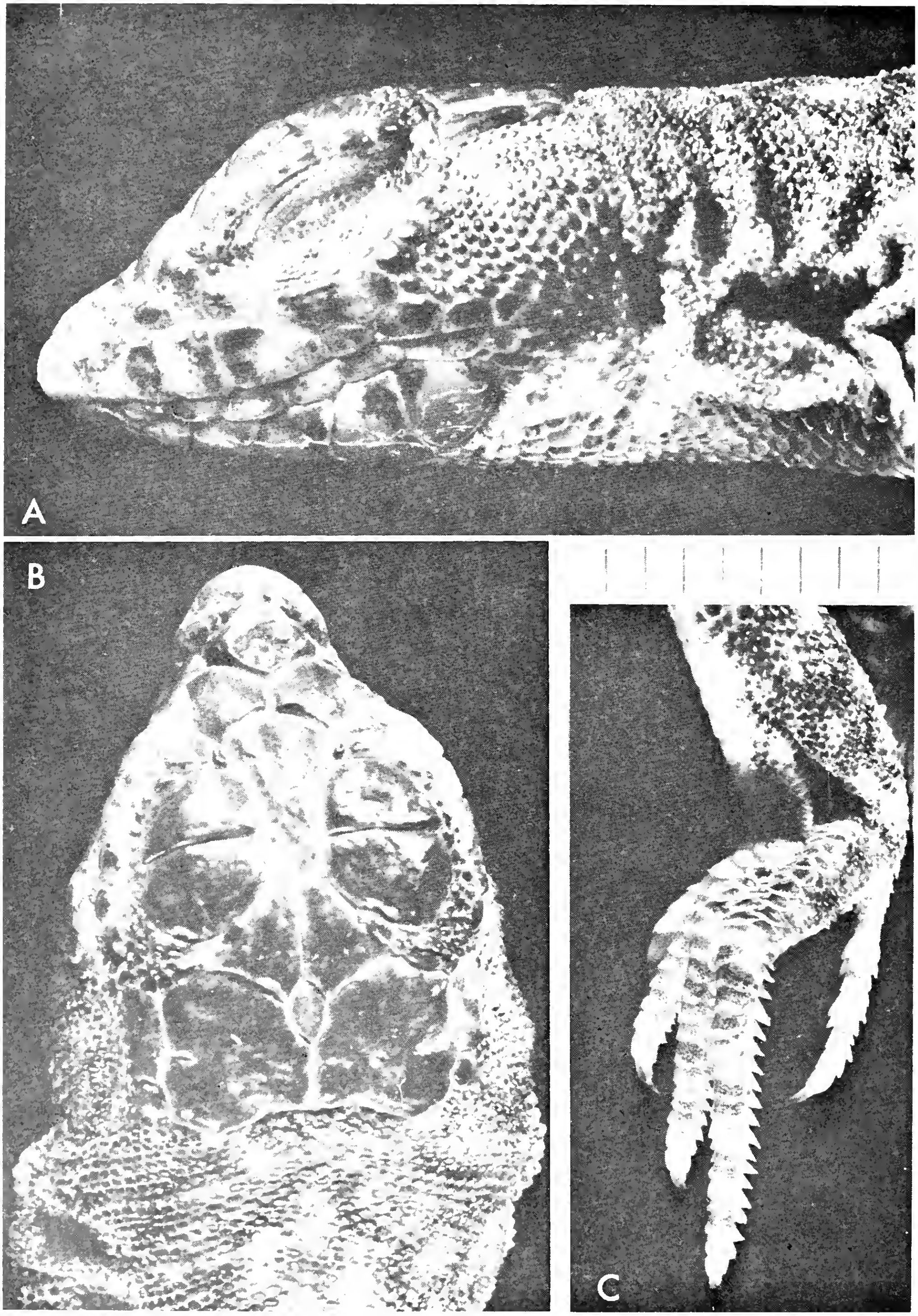

A
B
C

Plate 10. *Acanthodactylus robustus*, MCZ 56659.
A, Head, lateral view.
B, Head, dorsal view.
C, Left foot.
All at the same magnification. Scale: mm.

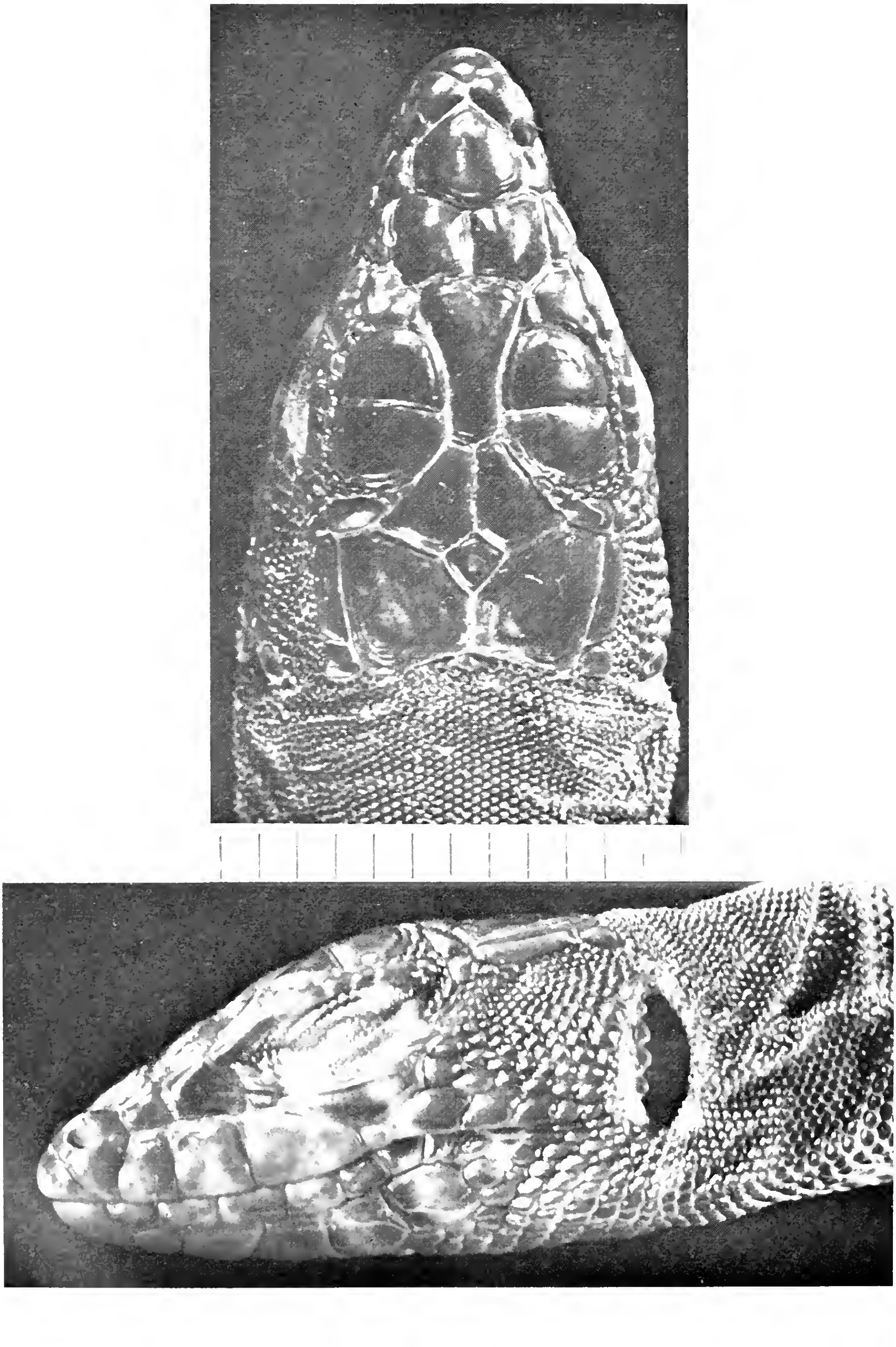


Plate 11. *Acanthodactylus grandis*, MCZ 56644, head. Above, dorsal view; Below, lateral view. Both at the same magnification. Scale: mm.

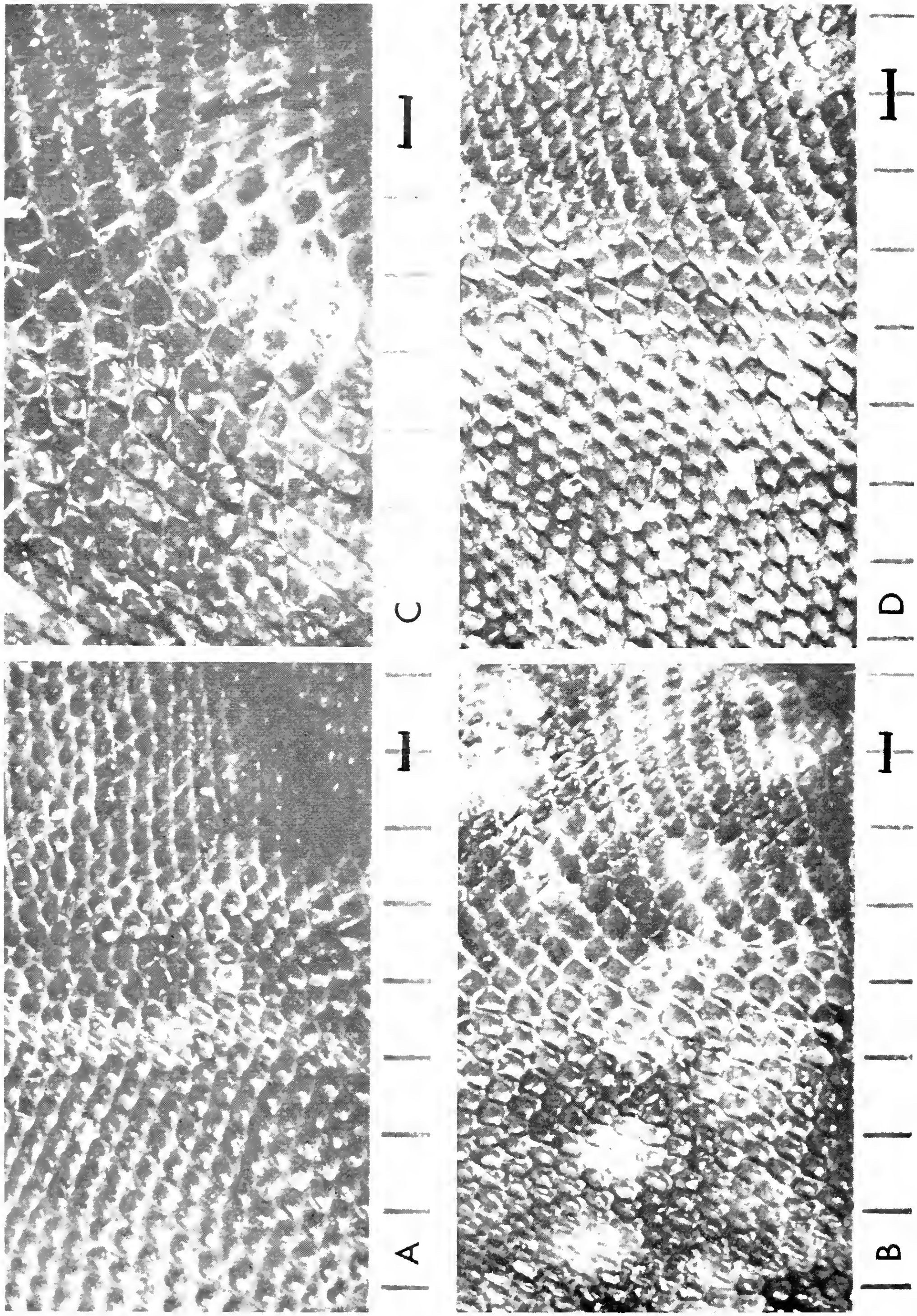

A
B
C
D

Plate 12. *Acanthodactylus* spp., middorsal scales of:

A, *A. scutellatus hardyi*, MCZ 56650.

B, *A. tristrami iracensis*, MCZ 56654.

C, *A. robustus*, MCZ 56649.

D, *A. grandis*, MCZ 56644.

Scales: mm. The horizontal scale bar (near the lower right of each figure) represents 1 per cent of the snout-vent length of each specimen.

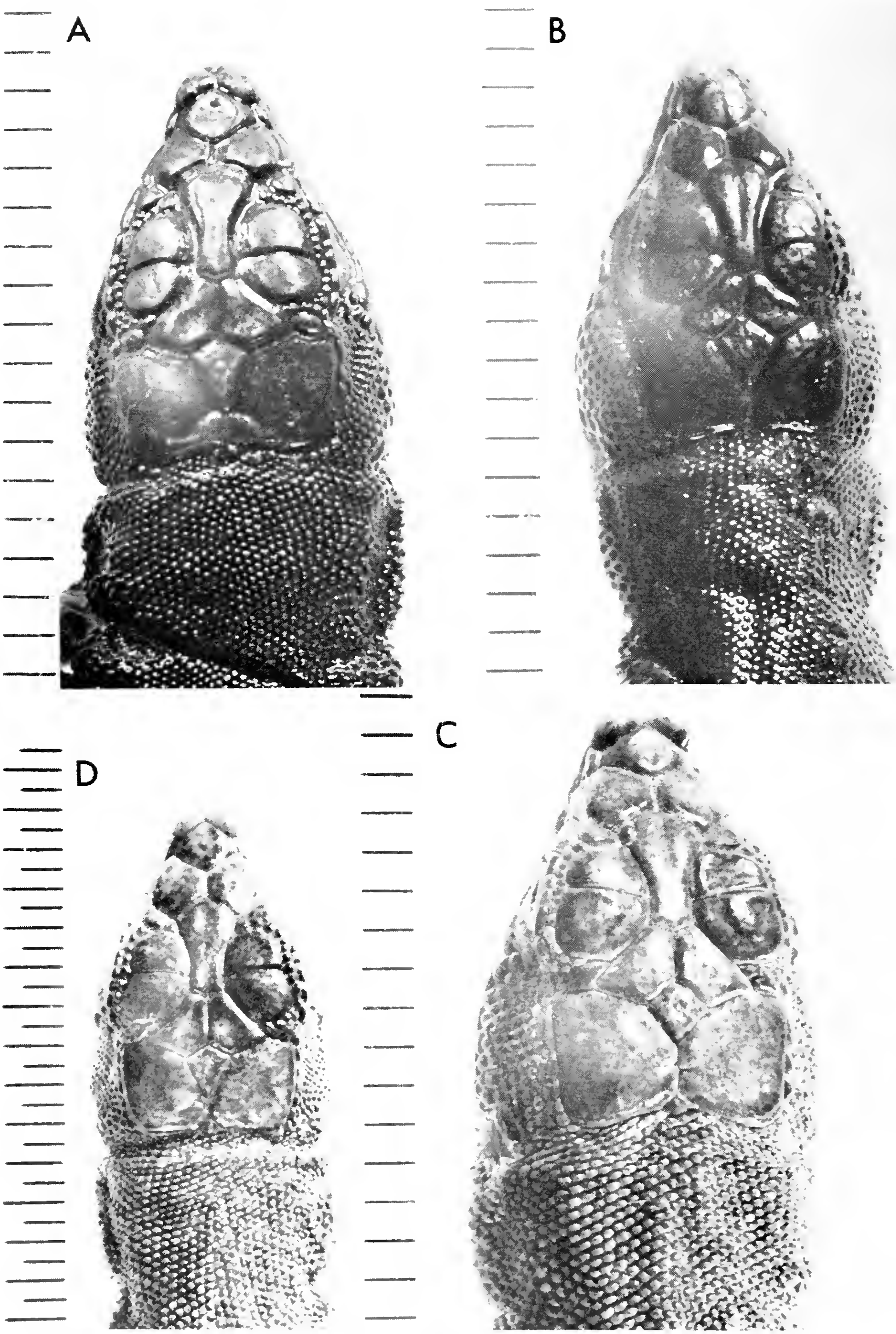

A
B
D
C

Plate 13. *Eremias brevirastris brevirostris*, head, dorsal view, af:
A, MCZ 56586, ♂ from northeastern Syria (snaut–vent: 50 mm).
B, MCZ 56588, from Iroq (Lake Habbaniya) (snaut–vent: 43 mm).
C, MCZ 56592, ♂ fram Iraq (Lake Habbaniya) (snout–vent: 60 mm).
D, MCZ 56571, ♀ from Saudi Arabia (snout–vent: 41 mm).
Scales: A, B, and C, mm; D, mm and half-mm.

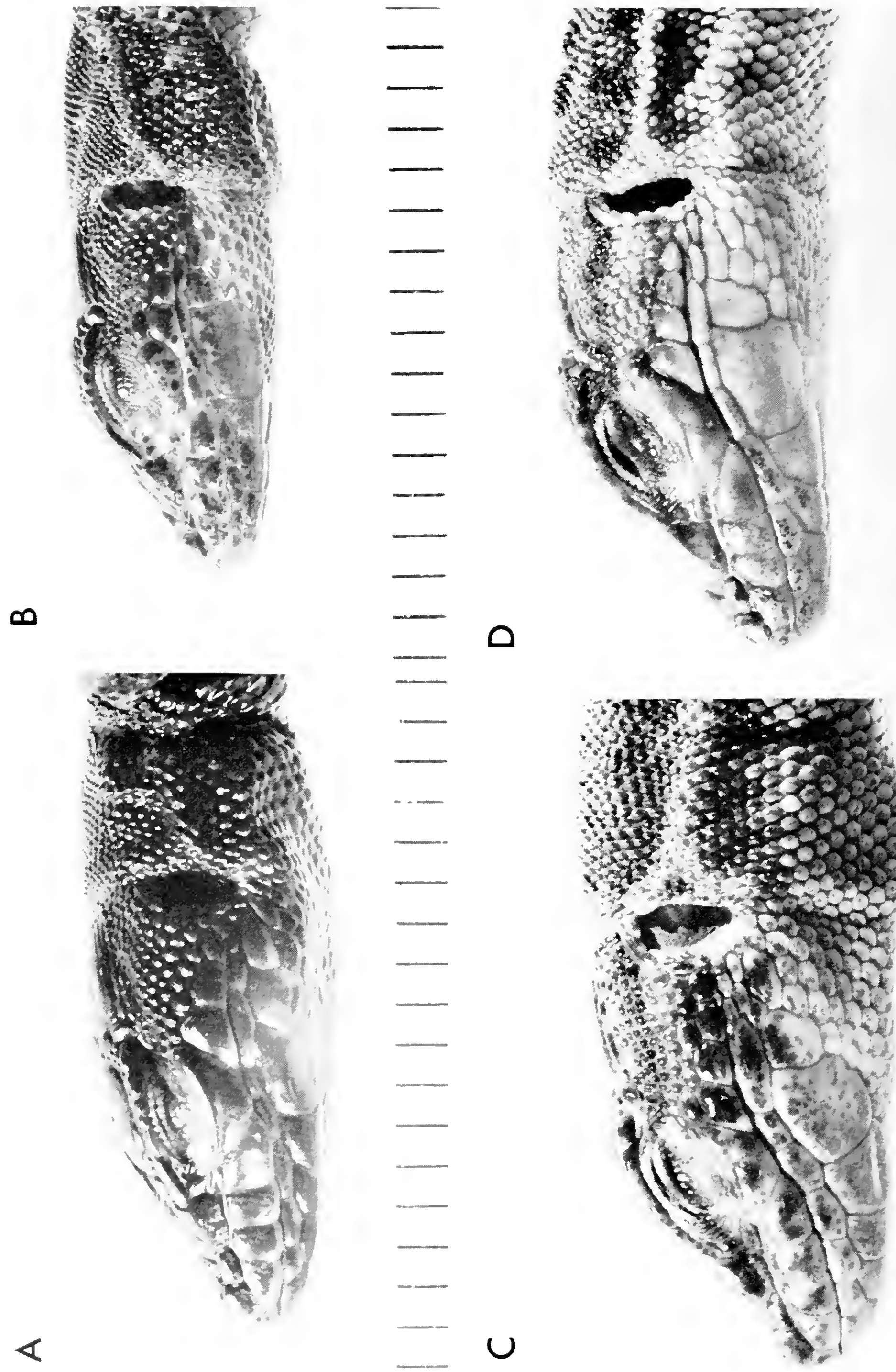

A
B
C
D

Plate 14. *Eremias brevirostris brevirostris*, head, lateral view, of:
A, MCZ 56586, ♂ from northeastern Syria (snout–vent: 50 mm).
B, MCZ 56587, ♀ from eastern Syria (snout–vent: 45 mm).
C, MCZ 56592, ♂ from Iraq (Lake Habbaniya) (snout–vent: 60 mm).
D, MCZ 56656, ♀ from Iraq (Station K-3) (snout–vent: 50 mm).
All at the same magnification. Scales: mm.

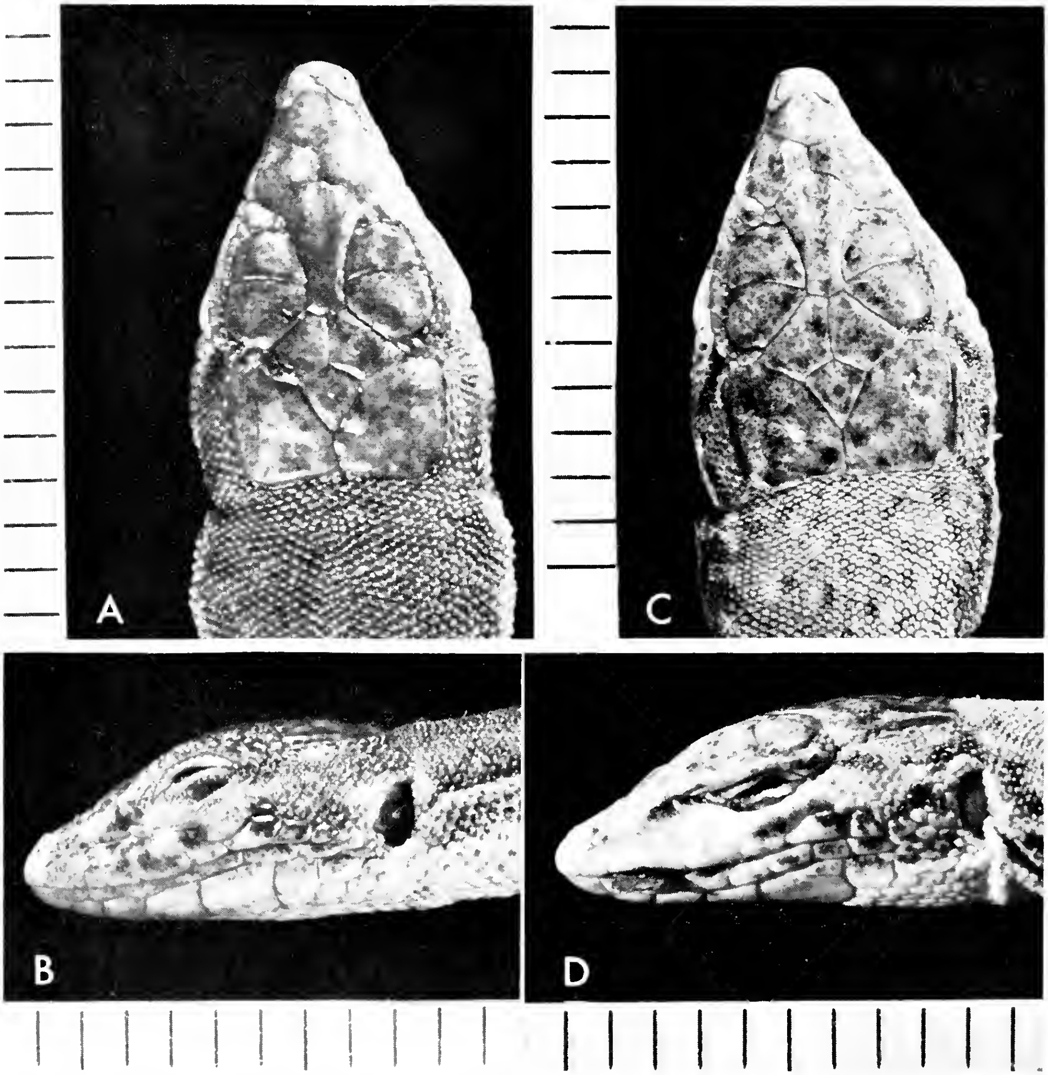


Plate 15. *Eremias brevirostris brevirostris*, head of:

A, MCZ 56567, ♂ from Saudi Arabia, dorsal view (snout–vent: 47 mm).

B, MCZ 56571, ♀ from Saudi Arabia, lateral view (snout–vent: 41 mm).

C, D, MCZ 54441, from West Pakistan (snout–vent: ca. 41 mm); C, dorsal view, D, lateral view.

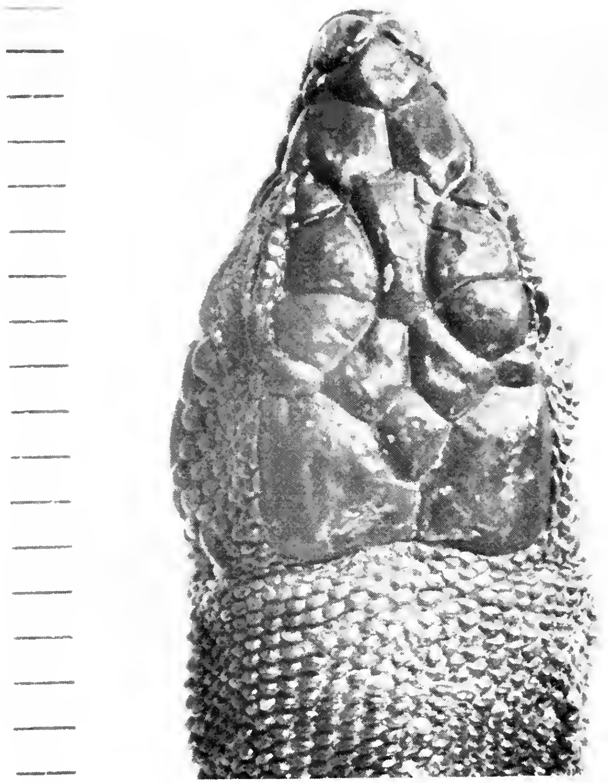


Plate 16. *Eremias brevirostris fieldi* subspec. nov., MCZ 56617, ♂, type (snout–vent 58 mm), head. Above, dorsal view; Below, lateral view. Both at the same magnification. Scale: mm.

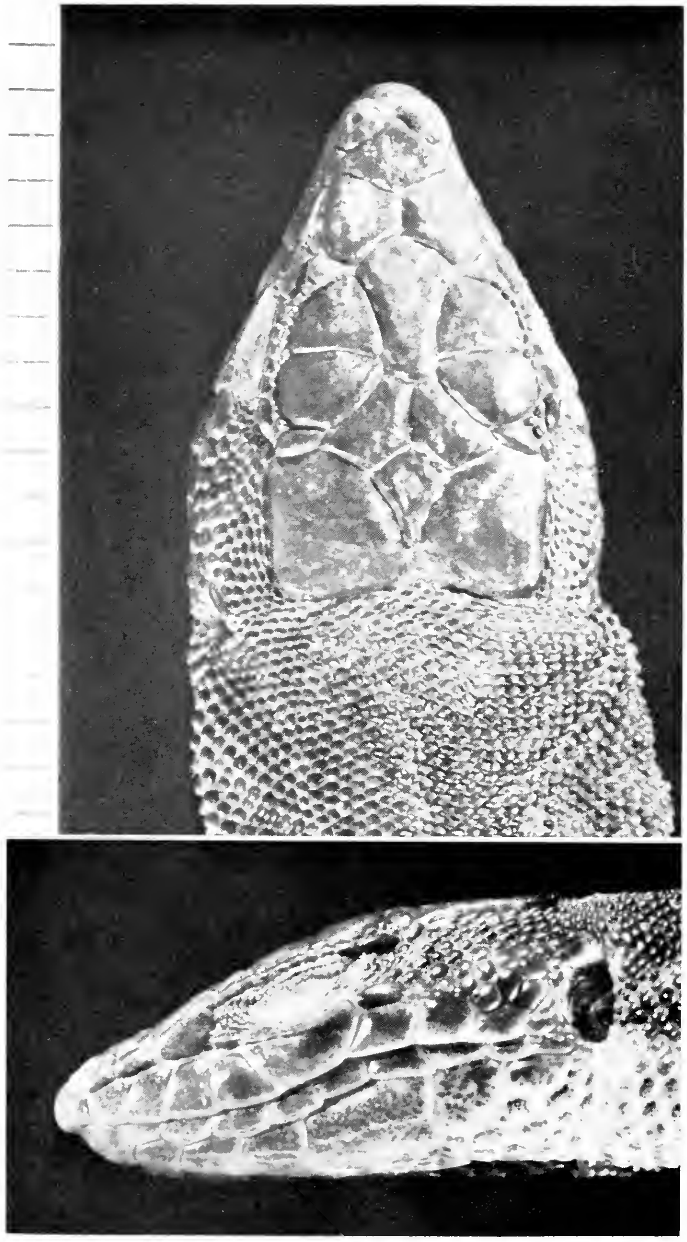


Plate 17. *Eremias brevirostris fieldi* subspec. nov., MCZ 56618, ♀ paratype (snout–vent: 61 mm), head. Above, dorsal view; Below, lateral view. Both at the same magnification. Scale: mm.

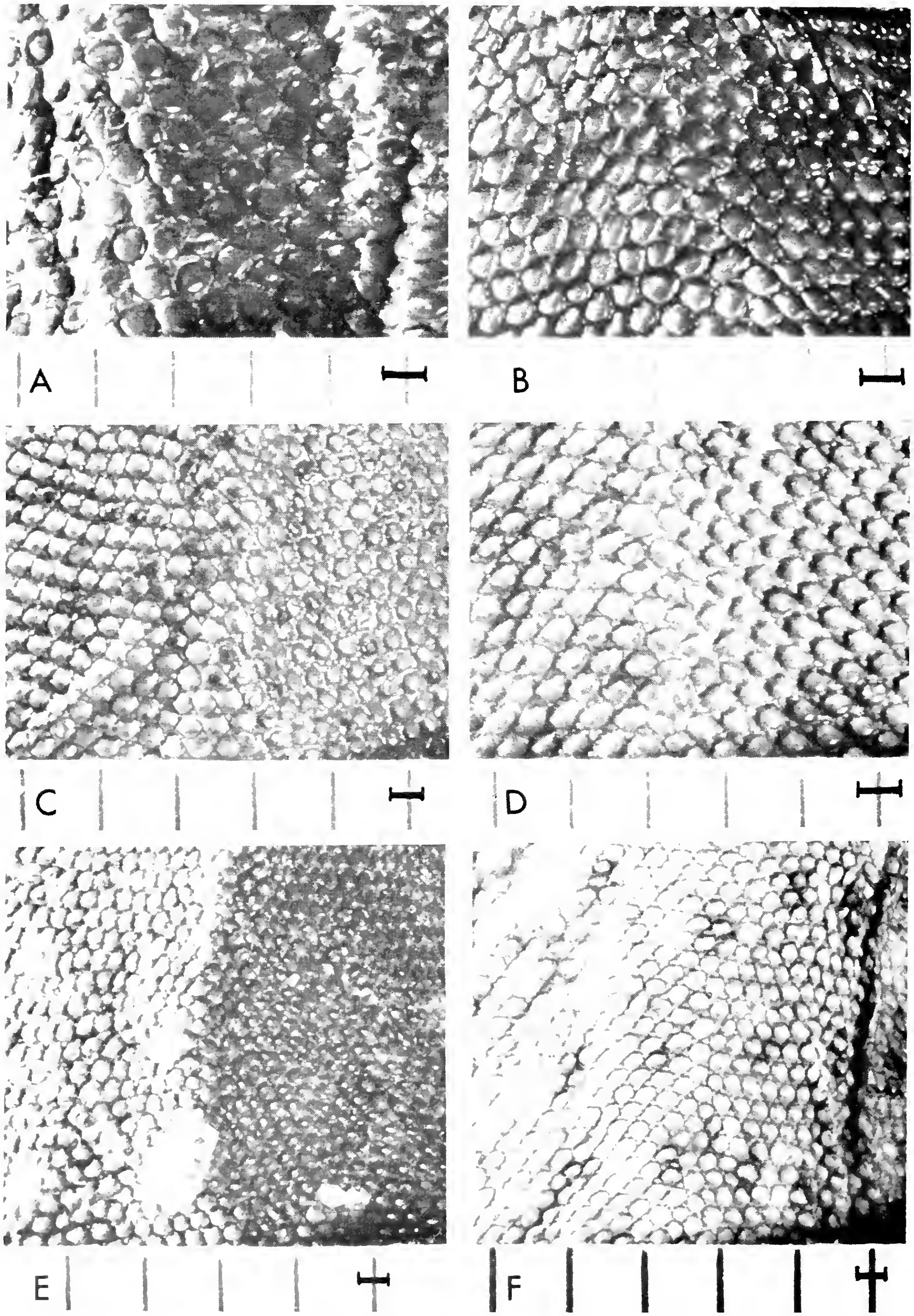

A
B
C
D
E
F

Plate 18. *Eremias brevirostris* sspp., middorsal scales of:

A, B, *E. b. fieldi*:

A, MCZ 56618, ♀ paratype.

B, MCZ 56617, ♂, type.

C–F, *E. b. brevirostris*:

C, MCZ 56567, ♂ from Arabia.

D, MCZ 56592, ♂ from Iraq.

E, MCZ 56587, ♀ from Syria.

F, MCZ 54441, from West Pakistan.

Scales: mm. The horizontal scale bar (near the lower right of each figure) represents 1 per cent of the snout–vent length of each specimen.

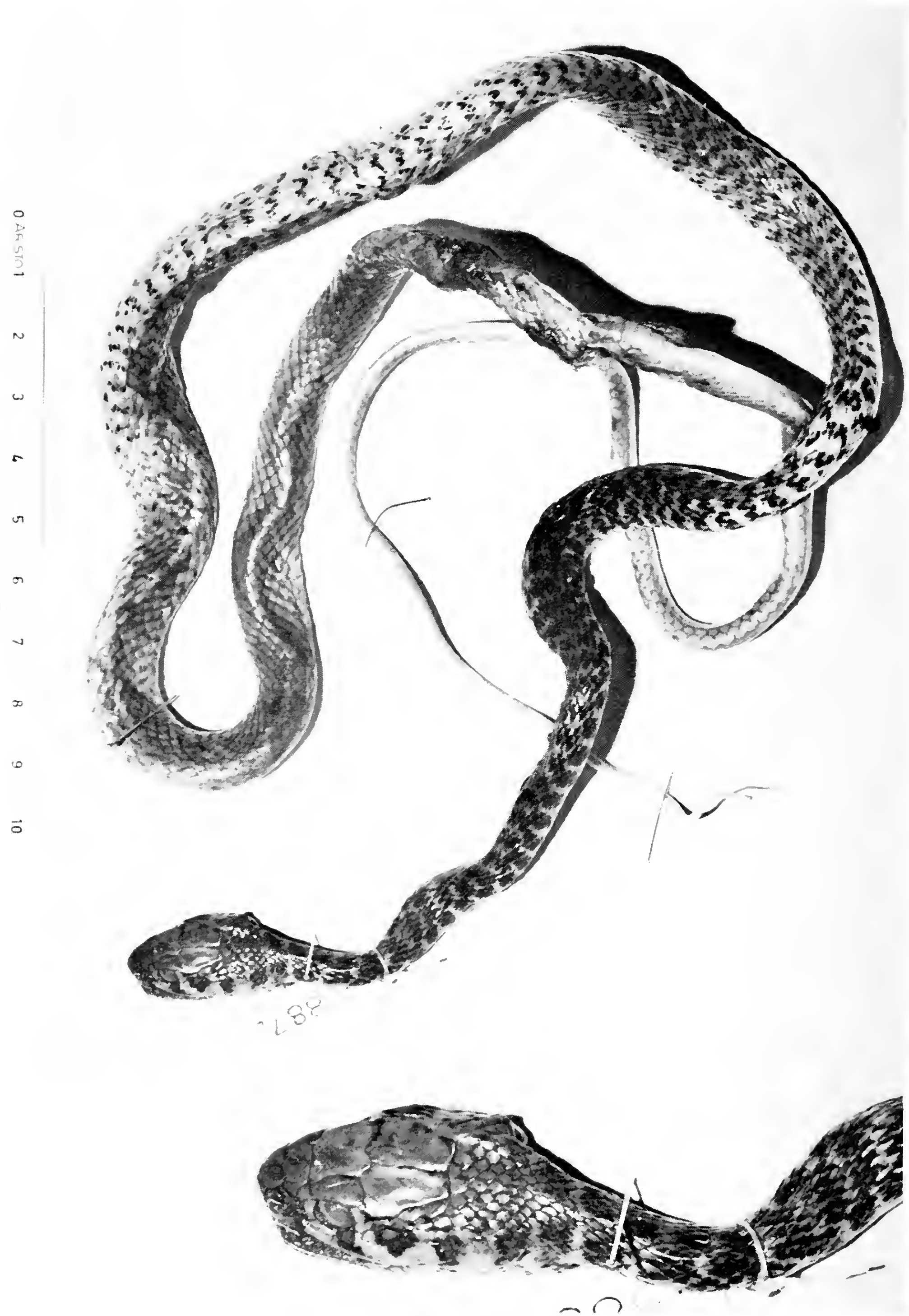

0 AE STO 1 2 3 4 5 6 7 8 9 10

Plate 19. *Coluber rhodorachis rhodorachis*, MCZ 58872, from Iran (Mahor Birinji): Above, whole specimen; Below, head, dorsolateral view. Scale: cm and mm.

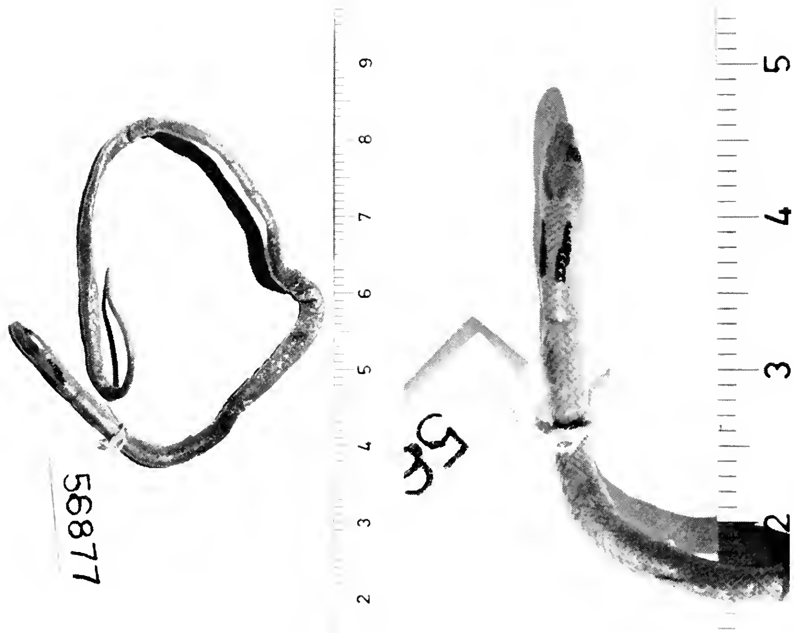


Plate 20. *Rhynchocalamus* sp., MCZ 56877, from Iran (Shalgahi): Left, whole specimen; Right, head, dorsolateral view. Scales: cm and mm.

Plate 21. *Walterinnesia aegyptia*, MCZ 56878, from Iran (Mahor Birinji). Scale: cm and mm.

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An Evolutionary Microcosm: Pleistocene and Recent History of the Land Snail *P. (Poecilozonites)* in Bermuda

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X-ray photograph of *Poecilozonites superior arenicolus.* Specimen from Bermuda Museum; locality unknown. Photograph courtesy of David M. Raup. Actual width of specimen is 37 mm.

AN EVOLUTIONARY MICROCOSM: PLEISTOCENE AND RECENT HISTORY OF THE LAND SNAIL P. (*POECILOZONITES*) IN BERMUDA

STEPHEN JAY GOULD

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ABSTRACT

Poecilozonites, an endemic element of the Bermudian waif biota, is a remarkable genus of pulmonate land snails that has undergone an adaptive radiation comparable in scope with the classic insular speciation and ecologic differentiation of Darwin's finches. This study considers all Pleistocene and Recent taxa of the subgenus P. (*Poecilozonites*) and represents an attempt to treat evolutionary problems with the techniques of multivariate biometry.

The ontogeny of *Poecilozonites* is characterized by complex allometric trends generated by the interplay of protoconch

dimensions and post-natal growth gradients. Comparisons among samples must be based upon non-redundant variables considered at a uniform shell size; techniques are presented for reducing raw data to meet these specifications.

An alternating sequence of glacial red soils and interglacial carbonates forms the geologic column of Pleistocene Bermuda. Red soils represent weathering at times of low sea level when modern Bermuda was at the interior of a land mass ten times its present size. Marine and eolian carbonates reflect the high sea levels of interglacial periods.

The polytypic species *P. cupula* includes three former "species"—*P. cupula cupula* (Gulick), *P. cupula dalli* (Gulick), and *P. cupula cupuloides* (Peile)—and two new forms—*P. cupula triangularis* and *P. cupula multispira*. These taxa conform to modern requirements for subspecies: each is morphologically distinct, continuously distributed in time, and uniquely located in a segment of the species range shared by no other conspecific form. Four subspecies exhibit a four-state color polymorphism; the fifth, *P. cupula cupula,* probably evolved from a local population of *P. cupula cupuloides* that had stabilized the most intensely colored morph. This supposition is supported by the pervasive positive correlation between size and color intensity; *P. c. cupula* is largest among the subspecies, while shells of the strongly colored morph exceed others in size both within and among local populations of *P. c. cupuloides.* The species became extinct about 120,000 years ago when Bermuda was nearly inundated by a eustatic rise that exceeded the present sea level by 20 meters.

The typological compendium of shapes that formed the previous classification of giant *P. nelsoni* is superseded by an arrangement based on criteria of the biological species concept. The geographic distribution of morphological variation within red-soil samples indicates that all belong to a single subspecies, *P. nelsoni nelsoni* (Bland). The smaller thick-shelled eolianite form, *P. nelsoni callosus* Gulick, is found in strata sandwiched between the two red soils in which *P. n. nelsoni* occurs. The literal interpretation of chronological subspecies in zig-zag evolution is not accepted; the two taxa are geographic subspecies, migrating with their preferred environments. A closely allied species, *P. superior* sp. nov., lived sympatrically with *P. nelsoni;* it too developed red-soil (*P. s. superior* subsp. nov.) and eolianite (*P. s. arenicolus* subsp. nov.) forms. The eolianite taxa of both species display a set of features adapted to warm interglacial climates and high calcium content of the carbonate dunes.

During the last 300,000 years, the conservative, central stock of *P. bermudensis* (*P. b. zonatus* Verrill) has given rise, in iterative fashion, to four similar, paedomorphic offshoots: *P. b. fasolti, P. b. sieglindae, P. b. seigmundi* (all new), and *P. b. bermudensis* (Pfeiffer). At adult sizes, each is, in comparison with the central stock, more weakly colored, thinner shelled, relatively wider, and more weakly domed; these are the outstanding juvenile features of *P. b. zonatus.* The paedomorphs are distinct genetic entities, not environmentally produced variants: they arise at the periphery of ancestral geographic ranges and lose genes that characterize adult stages of their non-paedomorphic progenitors. The adaptive significance of paedomorphosis may be related to the advantages of thin shells in the low calcium environment of red soils. No paedomorphs evolved in dune environments while the most intensely paedomorphic species developed in red soils.

In addition to branching, *P. bermudensis zonatus* itself displays fluctuating trends in morphology that correspond to ice-age climatic oscillations. Shells are thinner and smaller at a given whorl number in red soils, thicker and larger in eolianites. Modern land snails, exposed to a climatic

range similar to that of the Bermudian Pleistocene, exhibit the same trends in shell form. Again, the thin shells of red soils reflect an environmental deficiency of calcium for shell construction.

P. bermudensis and *P. cupula*, although widely overlapping in range, occupied different ecological realms and did not ordinarily inhabit the same locale. The two known instances of contact produced interspecific hybrids.

PREFACE

My first meeting with *Poecilozonites* was an accident. While rummaging through the fossil collection of Antioch College in 1962, I was attracted to a 1944 newspaper headline—"Red Army Drives for Warsaw"—and found the R. W. Sayles collection of Bermudian snails underneath. I resolved to study this remarkably diversified endemic genus and, after the usual scaling down of initial plans, produced a Ph.D. dissertation on the species *P. cupula* and *P. bermudensis* in 1967. To this, I have now added studies of *P. nelsoni* and *P. superior,* thus completing the subgenus *P.* (*Poecilozonites*). I have collected snails from all known Bermudian localities and have seen the museum collections of all previous workers.

Quantitative techniques were indispensable in deciphering the evolutionary history of this subgenus. I used 44 variables to characterize 1560 specimens and examined thousands more. The techniques, though suitable for numerical taxonomy, are used here for another purpose—to extract evolutionary data from shells belonging to well-established taxa.

Five evolutionary essays (Chapters 5–10) form the heart of this work. I have tried to structure each essay about a major issue in the evolutionary biology of pulmonates (the nomenclature and cause of exuberant morphological diversity in Chapter 6, the biospecies in paleontology in Chapter 7, the relationship of form and environment in Chapter 9). I hope that readers lacking time for the entire work will concentrate on these essays. In this expectation, I have tried to give them a dual status—as part of a unified whole and as independent entities. To enhance the second role, I have eliminated terminology depending on earlier chapters (computer code names for variables, for example) and have minimized the necessary preliminary reading (only Chapters 2A, 4, and 5A need be skimmed first).

It is easy, after a work is completed, to see its shortcomings. My quantitative comparisons among samples, for example, are based only upon differences among means. While variances were used to test the statistical significance of mean differences for all major conclusions, this use of variance as a tool does not exploit its full potentiality, for differences in variation may be as important as differences in means. It is only our residual typological bias that directs us to the latter path. In 1903, Gulick noted, quite correctly, that a major difference between *P. nelsoni callosus* and *P. nelsoni nelsoni* lay in the lowered variability of spire height in the former.

I am especially indebted to my teachers and advisors at Columbia University: R. L. Batten, J. Imbrie, N. D. Newell, B. Schaeffer. T. R. Waller adapted his program DASAN for my use; had I known the magnitude of required effort, I would not have dared to make the request. R. Turner kindly aided me in dissections. W. S. Broecker and D. Thurber supplied radiochemical dates. The curators of several museums have provided both hospitality and specimens: R. T. Abbott and R. Robertson of the Philadelphia Academy of Natural Sciences, J. F. White of Antioch College, L. Mowbray and F. Higgenbottom of the Bermuda Museum, W. Clench of the Museum of Comparative Zoology, C. MacClintock of Yale University, N. D. Newell and R. L. Batten of the American Museum of Natural History. W. Sutcliffe, director of the Bermuda Biological Station,

opened the facilities of that institution to me. This work is Contribution No. 466 of the Bermuda Biological Station, supported, in part, by N.S.F. grant GA901. F. T. Mackenzie and L. Land spent three summers puzzling over problems of Bermudian geology with me. I was aided in field collecting by F. T. Mackenzie, L. Land, G. Greiner, G. Brunskill, M. Hamilton, and a host of Bermudian children who curiously watched and sometimes aided while a stranger hammered at their roadcuts. I particularly thank the anonymous four-year-old who found the type specimen of *P. cupula multispira*. K. E. Chave, R. Schmalz, H. B. Rollins, and N. Eldredge have contributed valuable suggestions. M. Rosenberg, R. Houston, C. Jones, and S. Brocoum compensated for my artistic inadequacies by preparing the figures. I thank R. Adlington for photography and E. Gould and A. Pilot for typing various drafts of the manuscript. The traditional *mea culpa* for remaining errors applies, of course.

I. INTRODUCTION

A) Time in Paleontology

Paleontologists like myself who were attracted to their profession by the excitement of evolutionary theory are often chided by other evolutionists for entering an "unproductive" area of the field. The difficulty of drawing sound conclusions from material so inherently limited is often discouraging, so much so that were it not for one unique attribute, I doubt that many evolutionists would seriously consider the study of paleontology. That attribute is, of course, time. I doubt that principles derived from studies of living populations carried out in the course of a man's lifetime can provide a completely satisfactory model for processes occurring during the millennia that elapse in the history of nearly every significant phylogenetic event. At the least, paleontologists must be consulted to assess the consistency of principles derived from studies of living animals with the events of life's history; at best, direct consideration of the fourth dimension will provide new themes. An incorporation of insights gained from the study of vast time spans might increase the generality of evolutionary theory in much the same way that a consideration of high velocities modified Newtonian physics.

If time, in the sense of duration, is the desired quantity, then chronological placement of this segment assumes no great importance—1/2 million years of the Pliocene seems as desirable as an equal slice of the Cambrian. Given the inherent difficulties of paleontological studies, a time slice as close as possible to the present presents many strong advantages; preservation of fossils is apt to be good and closely related living populations provide a rich source for genetic and ecologic inferences.

B) An Evolutionary Microcosm

I have chosen a small time slice, a period bounded by the present and extending back into the Pleistocene no further than 500,000 years. Furthermore, this study is restricted to a subgenus of land snails endemic to the Bermuda Islands, now 19¼ square miles in area. Thus, the title of this work—An Evolutionary Microcosm. That such severe substantive limitation is often required for the abstraction of general conclusions seems ironic, but explanation of a phylogenetic event—the subsumption of its antecedent conditions under general laws of evolutionary theory—requires the reduction of those conditions to manageable proportions by the elimination of confusing variables. And it is from series of such explanations that general conclusions can be formulated concerning the operation of evolutionary processes in the history of life.

In this study, the major advantages of a twofold substantive limitation are as follows:

1. Of a small time slice including the present:

a) Fine stratigraphic control can be at-

tained in Bermuda, where 10 formations (7 bearing abundant specimens of *Poecilozonites*) span no more than 1/2 million years. Very close approaches to contemporaneity in correlations are possible.

b) With the time separating samples in vertical sequences measured in years rather than millennia, the possibility of finding successional populations in true genetic continuity is greatly enhanced. Most phylogenies established from fossil data, on the other hand, are reasonable morphologic series whose major virtue compared with phylogenies derived from modern forms is not that true ancestors are discovered but rather that the inferred phylogeny is not inconsistent with temporal requirements for the actual sequence.

c) Specimens are widespread, abundant, easy to prepare, and excellently preserved. Preservation of coloration patterns, sufficiently rare in Paleozoic and Mesozoic fossils to warrant special notice (e.g., Foerste, 1930; Hayasaka, 1953; Stokes and Stifel, 1964), approaches 100 per cent in these snails. The invaluable nature of color markings in infraspecific studies of land snails is evident in all the major works of this century—the studies of *Cepaea* (reviewed in Harvey, 1964), *Partula* (Crampton, 1916, 1925, 1932), *Achatinella* (Gulick, 1905; Welch, 1938, 1942, 1958), and *Liguus* (Pilsbry, 1912). Pleistocene color patterns in land snails have been briefly considered by Diver (1929) and Owen (1963, 1965, 1966). Absence of the protoconch, a handicap requiring the use of dubious approximations in the estimate of whorl numbers (e.g., Young, 1952, and Sadlick and Nielson, 1963), is a great hindrance to the biometric study of Paleozoic snails. The importance both of protoconch variables themselves and of the precision gained in unambiguous specification of whorl number is evident in the recent monograph of Fischer, Rodda, and Dietrich (1964). Discernible protoconchs remain in more than 95 per cent of the Bermudian specimens.

d) One of the three species of *P.* (*Poecilozonites*) has living representatives. *P. bermudensis bermudensis* is easily reared and bred in the laboratory.

2. Of a small and isolated geographic area:

a) The effects of migration in the confounding of phyletic inferences is virtually removed. With the exception of some Pacific islands, Bermuda is as isolated a spot of land as anywhere on the globe; *Poecilozonites* is a highly distinct endemic genus whose ancestors reached Bermuda long before deposition of the preserved Pleistocene sequence. Migration is no minor problem. The two most famous invertebrate fossil phylogenies, those of the echinoid *Micraster* and the bivalve *Gryphaea*, have recently come under attack with claims that an inferred *in situ* evolutionary sequence is better interpreted as a migration of the "derived" form from another area. Thus, Nichols (1959) believes that *Micraster senonensis* invaded the range of *M. cortestudinarium* but did not split off from it; and Hallam (1962) attributes to migration from elsewhere the first appearance of *Gryphaea* in the Lias of Britain.

The elimination of confusing variables in island situations has been stressed by Miller (1966: 16): "We can see the events of extinction, supplanting and mixture which are so complex on continents as usually to defy interpretation. Island situations are akin to simple lab tests, and from them principles may be determined that are applicable to the whole evolutionary process that moves forward on the continents or in the ocean basins."

b) With a very few square miles to explore and abundant specimens widely distributed, collections cover a large percentage of the total inhabitable area. Hecht (1965: 309) remarked that "If the basic principle of allopatric speciation is true, then the particular difficulties of paleontological research can make it nearly impossible to demonstrate the origin of species by known processes of speciation." In certain cases, however, temporal and

geographic resolution in Bermuda is sufficient to demonstrate that phyletic splitting occurred at the periphery of species ranges.

C) Previous Studies of Pleistocene Pulmonates and Prospectus for this Work

Extensive and excellent studies of Pleistocene pulmonates have been undertaken by paleontologists who find in their distribution patterns a record of ice age climatic fluctuations. Although extinction is frequently observed, a surprising result of these studies is the extreme paucity of evidence for the origin of any new taxa, either by speciation or phyletic evolution, during the Pleistocene. According to F. C. Baker (1937: 72), "the majority of the species lived throughout the entire Pleistocene epoch with but little change." Franzen and Leonard (1947: 394) found that "the pupillids of Kansas and of the adjoining areas included in this study do not present a study of evolutionary progression." D. W. Taylor, in his monograph on western North American forms, could cite but one doubtful case of origination, the derivation of *Gastrocopta cristata* and *G. procera* from *G. franzenae* on the dubious criterion that the ancestor's "range of variation includes specimens similar to both of the recent species" (1960: 93). Taylor believes, however, that this split may have been pre-Pleistocene. Hibbard and Taylor (1960), studying (1960: 5) the "most nearly complete latest Cenozoic faunal succession that is known for a small area anywhere in the world," discovered only one tentative origin. the derivation of *Promenetus exacuous exacuous* from *P. exacuous kansasensis* during the late Pleistocene. Commenting further on this case, Taylor (1965: 605) notes that "this interpretation is entirely speculative; if valid, it would be the only exception to the statement that the effects of the Pleistocene have been entirely destructive, not creative, at the specific level." And further. (1965: 602) "The span of Pleistocene times has been brief compared to the duration of molluscan species as identified by shells." Lozek, the major European student of Pleistocene pulmonates, finds that extinction of some forms is the only stratigraphic (i.e., evolutionary) significance of these mollusks (1965).

I find this surprising, because modern studies would indicate that pulmonate land snails, with their small populations, sedentary habits, and rapid adaptive response to selective pressures of environment and predators, are unexcelled among metazoa as material for evolutionary investigation. Welch (1942), for example, described 75 subspecies and 60 geographic races of the Hawaiian tree snail *Achatinella apexfulva;* and though we may question the categorical ranking of his taxa, the diversity is real and cannot possibly represent a situation *in statu quo* since the Pliocene. We must therefore ask whether the discrepancy between Pleistocene and Recent studies is real or is an artifact of limitations in evidence or approach. A few arguments for real distinction may be advanced—most Pleistocene studies are of rather homogeneous continental areas, while many of the best-known modern forms inhabit island chains and have diversified in a manner characteristic of such habitats—but I believe that the following reasons strongly suggest that the observed differences are artificial:

1. A question of semantics: The criterion employed by paleontologists for recognition of evolutionary origin is specific or at least subspecific difference (variously defined) in shell morphology. Paleontologists have generally not looked for the patterns of infraspecific diversity that provide most of our evolutionary data on Recent land snails.

2. Definitions color thought: Given this criterion and the null result of its application, the paleontologist is encouraged to regard the Pleistocene land snail species as a static indicator of a specified environment.

3. A question of interests: Pleistocene climate and stratigraphy, rather than evolu-

tion, is the focus of interest brought to most of the paleontological studies.

4. Interests designate methodology: The quantitative methods required to discern patterns of infraspecific variation are not used by paleontologists, who employ an abundance approach to map the geographic distribution of static entities.

5. Material limitations: Much of the Pleistocene fossil material is not well suited to evolutionary study. Genetically significant infraspecific variation has been most often noted in patterns of coloration, not in the linear dimensions and ratios of gross morphology. If color is not preserved, many well-differentiated geographic isolates meriting taxonomic distinction under precepts of the biological species concept may be unrecognizable.

I do not want this list to be read as a criticism of previous paleontological endeavor. I merely point out that Pleistocene land snails have not yet been approached by paleontologists whose interests and methods are directed towards the gathering of data on the operation of evolutionary processes in time.

This study, then, is a probe in these evolutionary directions; it represents an attempt to deal with four questions which epitomize the types of description and explanation most relevant to such work:

1. Can coherent patterns of morphologic variation in space and time be defined [here quantitatively]?

2. Can an evolutionary history be inferred from these patterns?

3. Can the operation of definite evolutionary processes be identified as productive of this history? In other words, can the efficient cause of observed evolutionary changes be specified?

4. Can the adaptive advantage of modified morphologies be ascertained? [Here, in particular, is there a simple relation between such changes and climatic fluctuations of the Bermudian Pleistocene?] In other words, can the final cause of observed evolutionary changes be inferred?

II. BACKGROUND TO THIS STUDY

A) The Geology of Bermuda

> Malacological problems must be solved within the framework of geology.
>
> Lozek, 1965: 205

Since the geological work of Land, Mackenzie, and myself has appeared elsewhere (Land, Mackenzie, and Gould, 1967), this section will contain only a general statement, a geologic section and those details required as background to the *Poecilozonites* study.

The Pleistocene sequence of Bermuda is a complex alternating and intertonguing series of marine limestones (shallow water and intertidal), wind-deposited carbonate dunes (eolianites), and red soils. *Poecilozonites* is found in the eolianites and red soils, being particularly abundant in unindurated zones of the eolianites (areas vegetated during pauses in dune accumulation). Few snails lived in the inhospitable dunes and few shells survived the solutional weathering which occurred after burial in red soils.

The challenge of Bermudian geology is to interpret these environments of deposition in terms of a synthesizing concept or independent variable—the rise and fall of the Pleistocene sea.

Sayles's (1931) idea that glacially-determined eustatic movements could account for the sequence of strata on Bermuda established a theme which, in Bretz's words (1960: 1753), "... probably will never be superseded." Eolianites and soils, which had not been given separate formational status by previous workers, became, for Sayles, the markers of glacial and interglacial times. He correlated times of eolianite formation with glacial episodes, suggesting that lowered sea level exposed a source of sand which, blown by strong winds and unimpeded by vegetation, migrated as desert dunes to form the present islands. Rising interglacial seas cut off the source of supply, and such periods were recorded by extensive soil formation.

Table 1. Stratigraphic column of Bermuda

Formation	Description	Interpretation
Recent	poorly developed brownish soil or crust	interglacial
Southampton	complex of eolianites and discontinuous unindurated zones	
St. George's	red paleosol of island wide extent	glacial
Spencer's Point	intertidal marine, beach and dune facies	
Pembroke	extensive eolianites and discontinuous unindurated zones	
Harrington	fairly continuous unindurated layer with shallow water marine and beach facies	interglacial
Devonshire	intertidal marine and poorly developed dune facies	
Shore Hills	well-developed red paleosol of island wide extent	glacial
Belmont	complex shallow water marine, beach and dune facies	interglacial
soil (?)	a reddened surface rarely seen in the Walsingham district	?glacial?
Walsingham	highly altered eolianites	interglacial

Sayles's stratigraphic column is the basis for that adopted here.

Bretz (1960) accepted the eustatic control of soil-eolianite alterations, but completely reversed Sayles's scheme. He proposed that " . . . the Bermuda dunes are coastal deposits, tied closely to their source of sand, the beach. Their fixation was prompt because of incipient cementation. They did not wander inland" (p. 1747). The substitution by Bretz of rapidly-cemented coastal dunes for Sayles's migrating desert dunes leads to a correlation of eolianite deposition with the high sea stands of interglacial periods. During glacial times, when the sea stood a few hundred feet below the present platform, soils formed over the area of modern Bermuda.

The stratigraphic column of Bermuda is presented as Table 1. The following notations summarize the Pleistocene history of Bermuda in the context of these formational names.

Walsingham: The Walsingham Formation, a complex of eolianites, underlies Belmont marine limestone in many areas of the Walsingham district (best seen at locality 5—Government Quarry—see Fig. 1 for a map of Bermuda). A reddish soil of unknown significance makes up part of the Walsingham complex at localities 5 and 9. The soil seems too persistent and strongly developed to represent a mere pause in dune accumulation, yet it lacks the depth of weathering and strong solutional features associated with red soils formed during glacial periods. Walsingham rocks underwent diagenesis prior to Belmont deposition (highly altered Walsingham clasts in uncemented Belmont conglomerate at locality 5). Thus, a glacial episode may separate the Walsingham and Belmont formations.

Belmont: The Belmont Formation is represented in most areas of its outcrop by marine limestones standing slightly above present sea level. At one time, however, the Belmont sea rose to +23 meters (marine conglomerate deposited against a sea cliff cut in Walsingham eolianite exposed at locality 5). Eolianites of Belmont age underlie and overlie the marine limestones in several places.

Shore Hills: The Shore Hills is the best developed red soil of Bermuda, reaching thicknesses of 12 feet in deep cylindrical solution pipes (popularly known as "palmetto stumps"). Snail shells are not abundant in the red, deeply weathered portions of the soil, having been destroyed by solution, but are fairly common in fissure fills of this age. All of Bermuda's extensive caves were cut during Shore Hills time, when percolating fresh water attacked the underlying carbonates.

Devonshire: The sea rose again to an elevation of +5 meters (wave cut notch at Hungry Bay, locality 49). The Devonshire Formation consists of intertidal sandy and conglomeratic deposits formed during this transgression. It is frequently found in erosional unconformity atop Belmont marine limestone, the Shore Hills soil having been stripped off. Radiochemical dates have been obtained from Devonshire corals (localities 2 and 51); each of four specimens indicates an approxi-

mate age of 120,000 years (W. S. Broecker, personal communication).

Harrington: The Harrington Formation, a poorly indurated calcarenite ("accretionary soil" of previous authors), formed as the Devonshire sea retreated. That it records a falling sea is indicated by the common vertical gradation from white sands with marine fossils at its base to brownish [carbon stained from terrestrial vegetation (?)] sands with abundant land snails at its top.

Pembroke: As the Devonshire sea continued to fall, carbonate detritus became available for deposition as Pembroke eolianite. Dune building was not continuous, since unindurated zones, representing pauses in dune accumulation, are common in this formation.

Spencer's Point: The sea rose again, certainly to +11 meters (east of locality 32) and possibly to +20 meters at Black Watch Pass (locality 6), depositing patchy intertidal conglomerates along the south shore and extensive marine and eolianite units on the north shore. A Spencer's Point coral obtained from a displaced block on Saucos Hill (locality 41) yielded a radiochemical date indistinguishable from those of Devonshire corals. This produces a stratigraphic puzzle to which three potential solutions may be offered:

1. The displaced block is Devonshire float. This can almost surely be discounted, since the block, weighing several tons, lies 10 feet downhill from Spencer's Point material of similar lithology. The nearest Devonshire is 1/2 mile to the west at Devonshire Bay.

2. There is only one post-Belmont marine limestone. The extensive unindurated zone lying below this coral and previously correlated with Harrington overlying Devonshire at Devonshire Bay belongs to a Belmont eolianite complex. Instead of one unindurated zone and two limestones, we have one limestone and two unindurated zones. This explanation seemed most probable until Mackenzie and Land found evidence of two limestones in superposition at Spencer's Point itself (locality 35).

3. Deposition of the entire Devonshire-Spencer's Point suite was so rapid that the 10–15 thousand-year uncertainty of the thorium dates does not allow a distinction of the limestones; the limestones would then represent two phases of a 120,000-year sea, evidence of which is now being uncovered in many areas (Broecker, 1966). Could the extensive Pembroke eolianites be deposited in so short an interval? Observations of the rapid growth of dunes active on Bermuda during the 19th century affirm this possibility. Thomson described the dune movements in his *Challenger* volume (1877: 310–311):

> There is a wonderful 'sand glacier' at Elbow Bay . . . The sand has entirely filled up a valley and is steadily progressing inland in a mass about five-and-twenty feet thick . . . [One resident] was either too late in adopting precautionary measures, or perhaps submitted hopelessly to his fate, for all that now remains of his cottage is the top of one of the chimneys projecting above the white sand like a tombstone.

St. George's: Although the St. George's soil is not as well developed as the underlying Shore Hills, it too records a period of diagenesis during lowered sea levels of a glacial period.

Southampton: As the sea rose, a new period of dune building commenced. The Southampton Formation, a complex of eolianites and unindurated zones, reaches thicknesses of greater than 200 feet in southwest Bermuda. Much of southwest Bermuda is entirely Southampton in age; the main island has been accreting in that direction, the major source of Bermuda's winds (Mackenzie, 1964). No marine Southampton has ever been found (marine Pembroke is likewise unknown), and Southampton seas must have stood below the present level. (No evidence for Pleistocene tectonism has been uncovered on Bermuda, and the islands may represent a good "tide gauge" for the assessment of Pleistocene eustasy.)

Recent: Dunes active during the 19th century have become stabilized by vegetation. A brownish soil derived from weathered eolianite underlies many vegetated areas; bare stretches are covered by a solutional crust. Much modern topography reflects the depositional profile of Southampton dunes. Red soil is present in lowlands, which were never covered by Southampton dunes.

B) Natural History of Poecilozonites in Bermuda

The native Bermudian biota is a classic instance of the depauperate and disharmonious associations characteristic of isolated oceanic islands populated by chance dispersal from distant continental areas. Birds excepted, a small lizard of the genus *Eumeces* is the only native tetrapod (even the inevitable rat required human transport). Only one other large pulmonate — *Succinea* — is found as a fossil. Verrill's treatise (1901–1902) remains the major work on the Bermudian biota and its origin.

Of *Poecilozonites* itself, Pilsbry (1900: 494) had the following to say: "The endemic element (*Poecilozonites*) undoubtedly long antedated the other forms, as its

generic divergence and strong specific differentiation indicate. In all probability it was derived from the Eastern United States by some rarely efficient means of transport." A member of the Zonitidae, *Poecilozonites* most closely resembles North American species of *Gastrodonta* and *Ventridens* in its genitalia, but is extraordinary in lacking the pedal furrow supposedly characteristic of aulacopod pulmonates. Pilsbry (1924) assigns it subfamily rank.

In his dissection of the genitalia, Pilsbry (1889) found a cleft spermatheca, one branch of which originated at the base of the penis. He wrote (1889: 85): "The connection of the duct of the spermatheca with the penis is unique as far as I know, in the Pulmonata, and suggests the probability of self-impregnation." With the kind assistance of Dr. Ruth Turner, I have been able to verify this observation. The occurrence is not, however, unique. According to Taylor (1900: 371), the cleft spermatheca with penile branch is found in "the North American Gastrodontae," the supposed ancestors of *Poecilozonites*. Pilsbry's designation of the Gastrodontinae as ancestral, established primarily on shell form, is thus affirmed. Moreover, the capacity for self-impregnation may help to explain the success of *Poecilozonites* in establishing itself on Bermuda. More than the sheer accident of first arrival may be involved, since the chance introduction of any single individual is so much greater than that of a pair or pregnant snail.[1]

Its time of arrival is unknown and cannot be inferred by extrapolating rates of the last 300,000 years; for early in its history, *Poecilozonites* underwent a vigorous and presumably rapid adaptive radiation. When *Poecilozonites* is encountered in the oldest Bermudian formations, it is strikingly diversified into three subgenera and 15 species (Peile, 1926). These range in size from giant *P. nelsoni* (maximum diameter 46 mm) to small species of the subgenera *P.* (*Gastrelasmus*) and *P.* (*Discozonites*), which rarely exceed 5 mm in diameter. In their morphologic variety, the species of *Poecilozonites* provide an excellent parallel to such famous cases of insular diversity as Darwin's finches and the Hawaiian honeycreepers. I assume, continuing the parallel, that the various species of *Poecilozonites* filled a spectrum of ecologic roles occupied by several genera in continental areas. The ecologic and geographic situation of Bermuda provided just those conditions outlined by Carlquist (1966) as evocative of rapid evolution on islands: lack of competitors and predators, a broad range of ecologic opportunity, and numerous potential geographic barriers.[2]

The native biota of Bermuda has fared poorly under the onslaught of species introduced by man. The indigenous flora was ravaged by hogs late in the 16th century and by rats early in the 17th; the famous Bermuda "cedar," *Juniperus bermudiana*, was nearly destroyed in this century by a scale blight. The vulnerability of island biotas to introduced competitors is well known (Simpson, 1953: 296; Mayr, 1963: 74). Carlquist (1966: 21) writes of the Hawaiian flora: "Almost any introduced continental species of plant seems capable of replacing autochthonous species of comparable ecological requirements."

[1] In particular, the arrival of a very small immature snail might be sufficient to establish the species. The abundance of microgastropods in the Bermuda Pleistocene indicates that small forms have a vastly better chance of introduction. *Poecilozonites*, of course, does not normally reproduce by self-fertilization. I have often observed their elaborate copulation ritual. I shall soon be conducting experiments to determine whether a *P. bermudensis bermudensis*, isolated from the time of hatching, will impregnate itself.

[2] I have undertaken some rather casual experiments which indicate that the modern reptiles and amphibians of Bermuda, including the native *Eumeces*, would rather starve than eat a *Poecilozonites*. Birds constitute the most likely source of predation, though there is no evidence, either direct or indirect ("anvils," etc.) of such. Bermuda now consists of 6 major and scores of minor islands.

re 1. Outline map of Bermuda before air force and navy modifications of the shore line. From Sayles (1931). Dotted lines are parish boundaries. Localities are described in Appendix 2.

Of all introduced invertebrates, however, none have proved so troublesome as the pulmonate snails. *Polygyra*, unknown as a fossil in Bermuda, is now the most common land snail on the islands. In the late 1880's, the "spiral snail" *Ruminea decollata*, introduced by Governor Lefroy in 1876, was inflicting so much agricultural damage that the Bermudian Government sponsored a prize contest for the development of "efficaceous, expeditious and economical methods to effect its extermination." (Bermuda Historical Society Documents, Hamilton, Bermuda). Pilsbry (1900) expressed surprise that *Otala lactea* had not managed to intrude itself, but his statement was negatively prophetic in the light of a recent *Otala* invasion. Despite the local legend attributing its introduction to a wartime visit of General De Gaulle, the arrival of *Otala* dates from 1928 when snails "brought into the colony to be tried as a food . . . subsequently escaped from captivity" (Bennett and Hughes, 1959: 432). Dr. Hughes tells me that the specimens came from New York's Fulton Fish Market and won their liberty by crawling out of a paper bag left on the offender's porch. The speed of their spread was colossal. *Otala* is now omnipresent on Bermuda, though its numbers have been substantially reduced by the "cannibal snail" *Euglandina rosea*, introduced from Hawaii as a biological control in 1958 (Simmonds and Hughes, 1963).

The effect on *Poecilozonites* of human introductions and disruptions of the native biota has been profound. Although two species, *P. bermudensis* and *P. circumfirmatus* are still common in many areas, they are absent over a wide range of potential habitat and constitute a small fraction of the total pulmonate fauna.

The reduction from 15 Shore Hills species to a handful of survivors is not wholly the work of man and his agents. Many common Harrington-Pembroke taxa do not appear in the St. George's and later formations, and their extinction can probably be attributed to the intervening high Spencer's Point sea (20 meters above present mean sea level). But other taxa common as fossils in the latest Southampton dunes have never been found alive, and their elimination can probably be traced to man. In addition to competition from introduced snails, *Poecilozonites* species probably fared poorly during the hog and rat plagues which, if we are to believe the early writers, must be ranked in effect with the Australian rabbit invasion. Hogs were introduced, probably by Spanish pirates, in the 16th century and were abundant when the English arrived. The English brought rats, and the plague of 1614–1618 almost destroyed the early settlements. Governor Butler wrote at this time (in Verrill, 1902: 713–714): "They eate up the whole country before them, wheresoever they went, utterly devoureinge all the corne they mett with all in an instant; so that, in despight of all the catts sent from out of England, and the layeinges of poyson, the Governours often fireinges of the whole islands, to the huge waste of much excellent caedar timber, or whatsoever els could be devised against them, they every day more and more so multiplied and grew upon the poore amazed people." All, indeed might have been lost "had not God (who noe doubt hath an especiall worck in the peopling of thes partes with Christians), by his owne hand, in great mercy, swept them all away in an instant." Verrill (1902), taking a less apocalyptic view, attributes their death to starvation. Both hogs and rats will eat snails; rats are often a major pulmonate predator (Liat, 1966). According to Verrill, "probably many species of birds, reptiles, insects, snails, etc. were exterminated . . . by the hogs and rats."

The recent introductions of *Ruminea* and *Otala* have further reduced the numbers and variety of *Poecilozonites*. An elderly employee of the Bermuda Biological Station, a resident of St. David's Island, tells me that in her youth, before the *Otala*

invasion, *Poecilozonites* were collected in barrels and burnt. She claims to have seen none in the last decade. The Rev. Lane, winner of the *Ruminea* control prize contest, referred to the living *Poecilozonites* as "a degenerated family which has not upheld the stature of its progenitors" (Documents, Bermuda Historical Society). *Sic transit gloria.*

III. GOALS AND METHODS OF QUANTIFICATION

The very term zonitoid connotes an almost featureless shell. H. B. Baker, 1938, p. 6

Of all classes of organisms, the mollusks are perhaps the best adapted for the study of ontogenetic stages . . . since all these stages are preserved as a permanent record in the form of the shell.
Grabau, 1907, p. 609

A) Introduction

The first statement above is a challenge; the second, its partial resolution. A snail shell appears poor indeed when compared with a vertebrate skeleton for enumeration of measurable variables, yet it possesses other features particularly favorable for quantitative evolutionary studies.

1. As an accretionary structure, it retains a complete record of its morphological development. If shape changes during ontogeny, a general occurrence among pulmonates, then a description of the sequence of forms attained at various sizes or whorl numbers provides a basis for interpreting relationships between ontogeny and phylogeny: the size of origin of new features can be determined; phyletic alteration of form can be understood as the cumulative effect of ontogenetic changes in growth rates; paedomorphic or recapitulatory effects can easily be spotted. These possibilities were recognized by some early evolutionary paleontologists, but their approach was often marred by an *a priori* faith in the universality of Haeckelian recapitulation (e.g., Grabau, 1902, 1907).

2. The pulmonate shell is known to be highly expressive of the environmental conditions in which it grows (e.g., Rensch, 1932; Oldham, 1929, 1934). Given this phenotypic plasticity, it will be difficult to distinguish genetic from environmental modification, but selective forces in the environment can often be ascertained and their influence on larger changes with an inferred genetic basis determined.

Measurements have been used in the classic studies of pulmonate diversity (e.g., Crampton, 1916, 1925, 1932), but these have not extended beyond the "standard" dimensions (total length and width, apertural length and width) and derived ratios. Yet these measures of gross morphology have little discriminating power, since similar values are attained independently by population after population. Moreover, when only one set of measures is made per specimen, ontogeny must be inferred from mass curves (Gould, 1966a), thus frustrating the major advantage of studying pulmonate shells in the first place—the possibility of obtaining true longitudinal data, the only kind that can yield information on individual variation in growth (Cock, 1966: 136). Often, to make matters worse, attempts are made to infer ontogeny from curves constructed for a series of adults (among helicids, for example, which have a definite final size varying widely among individuals of a population). Yet, there is no reason why such curves should reflect individual ontogeny in any precise way (Röhrs, 1958, 1959, 1961; Gould, 1966b). This method represents a confusion of two different types of data—longitudinal and static (Cock, 1966).

I have tried to increase the number of variables beyond the conventional set of general size and shape measures in four ways: by the quantification of color variation; by the inclusion of protoconch dimensions; by expanding the set of apertural measures to encompass the many ontogenetic changes in shape not expressed in the width/height form ratio; and by measuring heights and widths at each whorl. The last of these four accomplishes two purposes:

1. A mathematical expression for the geometry of the dome may be derived from the width-height pairs; this expression abstracts the ontogeny of general shape development as a single statement.

2. Since zonitoids continue to grow throughout life and therefore lack terminal growth features defining adult dimensions (such as the expanded and colored lip of many helicids), meaningful size measures must be taken with reference to a whorl number, rather than a (indefinable adult) growth stage.

The resulting set of measures, 33 variables and 11 ratios and combinations, serve to define the form of *Poecilozonites* in sufficient detail to permit a fairly complete reconstruction of the shell from a table of the variables alone. Any important alteration in shell morphology should be capable of identification and definition within the set of measures, and a basis for multivariate comparisons among shells is provided.

Raup, in a series of fascinating papers (1961, 1962, 1965, 1966; see also Thompson, 1942: 748–849), has programmed a computer to generate the forms of coiled shells from four parameters—the shape of the generating curve, the whorl expansion rate, the position of the generating curve with respect to the axis of coiling, and the rate of whorl translation down that axis. Why, then, have more than 30 measures been used in this study?

1. Raup's model produces only the general form of the shell; 7 of my measures deal with color and shell thickness: "It should be emphasized that the four parameters do not completely describe the morphology of the coiled shell. . . . The model is concerned only with general form and includes only that ornamentation produced by the revolution of the generating curve about the axis" (Raup, 1966: 1181).

2. One of Raup's parameters, shape of the generating curve, is composite. In practice, it is drawn rather than defined mathematically when its shape does not approximate a simple geometric figure. To express the shape of a complex aperture in numbers, many variables are needed: I have used seven. "The generating curve is often equivalent to the outline of the growing edge of the shell. As such, its shape can only rarely be defined mathematically. . . . More generally, however, a line drawing is used to describe the shape" (Raup, 1966: 1179).

3. The protoconch (embryonic shell) is rarely constituted in geometric similarity with the rest of the shell as assumed by Raup's model. This introduces a small discrepancy, quite unimportant to Raup's analysis, between the apical regions of actual and computer-generated gastropod shapes. Three variables define protoconch form in this work.

4. Raup's model assumes that geometric similarity is preserved with shell growth. While many marine shells conform adequately to this criterion, significant allometry[1] is almost universal in pulmonates. (The characteristic domed shape, for example, implies that height increases faster than width—Gould, 1966a.) If the allometric trend is regular and gradual, it can often be encompassed within Raup's model by redefining one of the parameters as a variable instead of a constant; gradual decrease of the translation rate produces an "extraconical" shell (Raup, 1966: 1185). Two of my variables relate to the ontogeny of doming in *Poecilozonites*.

5. There is a fair amount of redundancy in my measures, some introduced inadvertently, the rest a by-product of variables needed to construct the derived parameters. Heights and widths at whorls 1 through 5 do not represent 10 independent sources of variation; they are all, however, utilized to define the allometric parameters of shell doming.

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[1] I use the term allometry to describe any size-correlated change of shape, not only those trends in form which can be adequately fitted by power functions (Gould, 1966b: 600–603).

TABLE 2. HYPOTHETICAL DATA MATRICES OF FORM USED IN THIS STUDY

Raw Data Matrices

	Protoconch Width	Width End of Whorl 5	Height End of Whorl 5
Sample 1:			
specimen 1	1.5	25	15
specimen 2	1.6	26	16
specimen 3	1.7	27	17

	Protoconch Width	Width End of Whorl 5	Height End of Whorl 5
Sample 2:			
specimen 1	1.6	26	16
specimen 2	1.7	27	17
specimen 3	1.8	28	18

Matrix of Means

	Protoconch Width	Width End of Whorl 5	Height End of Whorl 5
Sample 1	1.6	26	16
Sample 2	1.7	27	17

6. Our difference of approach reflects a difference of interests. Raup abstracts the general form of coiled shells with as few parameters as possible. Computers can then generate a range of possible forms; this allows us to consider such fundamental questions as: why do actual shells occupy only a part of the range of potential shapes? I am interested in detecting the subtle variations in morphology that characterize geographic variation and incipient differentiation within species.

B) Goals of Quantification in this Study

A data matrix may be treated in two ways: we make comparisons among rows or among columns. [In this study, each column is a variable, each row a specimen (or, in the matrices of means described below, the mean sample values for each variable).] Table 2 presents some simplified, hypothetical data matrices of the form used here.

1. Comparison among rows (specimens or samples): The morphological differences of specimens within and among samples constitute the primary data in any evolutionary study of form. Needham (1950) has suggested the heuristic statement: form = size + shape. Comparisons of "form" may be made on either basis.

a) Size: Size, to be a useful criterion, must be standardized in some way. This is usually achieved by comparing specimens at a definable growth stage, generally the adult. Zonitoids, as mentioned above, continue to grow throughout life. I have therefore been unable to use the maximum size of specimens as a basis for comparison,[1] and a different standard must be sought. Size at a given number of whorls, the usual alternative for zonitoids (Baker, 1938: 5), is used here. A criterion for numbering whorls must then be established, and it is a virtue of the *Poecilozonites* material that "the best and most accurate method" (Sadlick and Nielson, 1963: 1086), counting from the termination of the protoconch, is available. Burma (1948), Young (1952), and Sadlick and Neilson (1963), working with material in which the apical region is rarely found intact, were constrained to use another standard (a "zero point" at which the whorl height equals some arbitrary value). Although the zero point can be determined objectively, it lacks the desirable attribute of making the whorl numbering criterion coincident with a physiologically meaningful point in shell development. When the termination of the protoconch can be used, the zero point is the true beginning of post-hatching growth. Two disclaimers should be made for this method:

i) *Size at a whorl has no* a priori

[1] This inability is one of the most unfortunate aspects of this work; for maximum size surely varies among samples. The difficulty could be surmounted if the sample sizes were relatively equal and quite large, but too many of my samples are too small even to allow a randomized equalization of sample sizes at a "least common denominator" number.

relationship to the final dimensions attained by the shell. Large size at a given whorl is no guarantee of large final size.

ii) No definite implications of age or "relative age" (Burma, 1948) should be drawn from the whorl number, which serves primarily as a standard for comparison.

b) Shape: Shape is expressed as a dimensionless number (usually a ratio or an angle). The comparison of shape in specimens of different size is the reason usually cited for forming a ratio, but we must avoid the fallacious corollary that the ratio is therefore independent of size. If the relationship of variables forming the ratio is allometric, then the value of the ratio will change as size increases. Thus Franzen (1966) claims that the width/height ratio is useful in separating the succineid pulmonate species *Oxyloma salleana* and *O. retusa.* The ratio varies with size, however, and we are given no assurance that it can discriminate between the two species at a common size. For a single sample of *O. salleana,* mean width/height for specimens > 3 1/2 whorls is 0.654 (observed range, 0.608–0.695, N=4); for specimens < 3 whorls, mean width/height is 0.539 (observed range, 0.510–0.577, N=4).

Almost all bivariate plots of ontogeny in *Poecilozonites* are allometric, and *meaningful comparisons of shape must be made at equal sizes*[1] *or whorl numbers.* It is not easy to decide which of the two affords a better comparison. In *P. cupula,* differences in size-at-a-whorl among the various subspecies is so great that choosing a size of 17 mm, for example, would result in the comparison of a *P. cupula dalli* of 5 whorls with a *P. cupula cupula* of 4 whorls. Since many important alterations of shape occur during growth of the fifth whorl, the choice of 17 mm would occasion the comparison of a *P. cupula dalli* of near maximum (observed) size with a rather juvenile *P. cupula cupula.* Despite the above disclaimer (p. 423), whorl number in *P. cupula* is probably a better criterion of developmental stage than is size. If this is so, then the choice of equal size or equal whorl number as a standard for shape comparisons depends upon whether ontogenetic alteration of form is under the primary control of absolute size or developmental stage. Since definite shape changes tend to occur at similar whorl numbers rather than at a similar size in *P. cupula,* intersample shape comparisons are made at a common whorl number. In *P. bermudensis,* the problem is not so acute, since the size range at a whorl is quite small among samples.

When all variables have been standardized so that their values are recorded at a common size or whorl number, a basis for the meaningful comparison of form among samples is provided in the "matrix of means" (Table 2b), each row of which contains the mean sample value for each of the variables. The mean sample values are obtained in two ways, depending upon the nature of the variable. If the variable is already standardized (e.g., height at the third whorl, whorl number at which the upper color band is formed), a simple mean is calculated. Other measures, particularly the set of apertural variables, are not made at the standardized value, but are taken at the final size of each specimen. (Theoretically, each apertural variable could be measured at, say, the fifth whorl, but this would necessitate the breakage of all larger specimens and the discard of all smaller ones.) In such cases, the predicted value at the chosen common size or whorl number is determined by bivariate regression. The range of measured specimens is

[1] Size is defined here as width + height. Many ambiguities have been introduced by authors who use height or width alone as the measure of size. Price-Jones (1930), for example, claimed to have demonstrated that large adults of *Cepaea nemoralis* tend to have a high width/height ratio. But since he used total width as his criterion of total size, the positive correlation of "size" with width/height only shows that an adult with an absolutely wide shell tends also to be relatively wide.

selected so that the common size or whorl number is near the midpoint of the measured interval. Only shells of four whorls or more are used to construct the regressions, since a wider size range results in significant departures from linearity. Each variable is plotted against size or whorl number (depending upon the chosen criterion of comparison), and its estimated value at the chosen size or whorl number is determined.

The 810 reduced major axis fits (10 variables in each of 81 samples; 20 specimens per sample)[1] were calculated by DASAN, a FORTRAN 2 program written by Dr. T. R. Waller and kindly modified by him for use in this problem.

2. Comparison among columns (variables): Bivariate regression and correlation are standard methods for comparing variables with one another. When considered over a wide range of size, two variables generally display strong correlation for the trivial reason that most linear dimensions increase as an organism gets larger. Variables may be related for other reasons—similarity of function or mechanical proximity, for example—and it is the aim of correlation studies to provide a body of data from which the causal factors of variable interrelationships can be inferred (see Olson and Miller, 1958). A complete set of such interrelationships can be depicted in a matrix of correlation coefficients. Since the sheer quantity of information in such a matrix is too vast for consideration in raw form (there will be 780 meaningful entries when the interrelationships of 40 variables are assessed), multivariate clustering methods for the abstraction of simpler patterns implicit but difficult to recognize in the raw matrix must be used. Factor analysis, the abstracting method applied here, will be described in Chapter 5.

Differences of form provide the basis for assessing evolutionary relationships among populations. These differences are expressed in terms of variables. We study the interrelationship of variables for two reasons:

a) The recognition of differences in form is purely descriptive. The goal of evolutionary studies is to explain these differences. The study of interrelationships among variables may lead to an identification of causal influences shaping the form of an organism. In a study of pelycosaurian reptiles, for example, I found that widths of limb bones and vertebrae correlated more strongly with one another than with their respective lengths (Gould, 1967). Two major clusters of variables, bone lengths and bone widths, were abstracted from the correlation matrix. Total body length sorted with the bone lengths, estimated weight with the widths. Since terrestrial vertebrates compensate increasing weight by differential thickening of bones responsible for support, the clusters could be explained in mechanical terms. The increased relative thickness of supporting bones in large pelycosaurs is an adaptive response to increased size.

b) Redundancies can be eliminated: The major difficulty plaguing a proper evaluation of the differences in form among samples is failure to account for interrelationships among variables. Two populations are often said to be very distinct because they differ significantly in 20 characters. Built into this statement, however, is the hidden major premise that the 20 characters reflect 20 separate determinants of variation. This premise will usually be false. In extreme cases, the 20 characters will form a tight cluster measuring only one significant dimension of difference. Given the prevalence of allometric trends in ontogeny, phyletic size increase without alteration of ancestral ontogenetic trends will produce an organism differing

[1] For a few populations, fewer than 20 specimens were available. For samples with abundant specimens (the large majority), all individuals larger than 4 whorls were selected. These specimens were divided into two lots on the basis of size and 10 specimens were randomly chosen from each lot.

from its ancestor in many aspects of shape. The total genetic difference (the ideal basis for assigning taxonomic rank to ancestor and descendant) may be very small or even nil. Corbet (1964) found that the contrast in skull form between island and mainland populations of the bank vole *Clethrionomys glareolus* was a consequence of size differences: "The number of independent characters distinguishing the island races is very small" (1964: 191). Former hypotheses of relict distribution, once deemed necessary from the supposed intensity of genetic divergence implied by differences in skull shape, are not required and the pattern of variation is compatible with a hypothesis of recent accidental introduction from the mainland. In *Poecilozonites*, large relative width and wide umbilicus at a standard whorl number are mechanically correlated. Only one significant dimension of variability is expressed by the two measures.

C) *The Variables and their Measurement*

In this listing, each variable is defined and its method of measurement given in the following format: name of the variable, its computer code name, and a description of the method of measurement if not obvious.

1. Standardized Variables:

a) Color

1, 2. Whorl number of formation of upper and lower color bands on the upper whorl surface, ONESEUP, ONSELO. Color deposition begins as discontinuous blotches and flames. These variables record the whorl number at which the transition from blotches to a solid band occurs.

3, 4, 5. Percentage of upper whorl surface covered by color bands at the third, fourth and fifth whorl, COLOR3, COLOR4, COLOR5. The width of the upper whorl surface and the width of the color bands on this surface are measured. A ratio is formed: width of color bands/total width of upper whorl surface.

6. Percentage of the lower whorl surface covered by the subperipheral color band at the fifth whorl, LOWCOL. As above, but on lower whorl surface. This measurement cannot be made if the specimen has fewer than 5 or greater than 6 whorls. (In the latter case, the lower whorl surface is covered by the succeeding whorl; the upper whorl surface remains completely exposed in all whorls of *Poecilozonites.*)

b) Protoconch

7. Width of the protoconch, PRWIDT.

8. Height of the protoconch, PRHIGH. Actually, the height of the protoconch spire; that part of the protoconch below the whorl periphery is covered by succeeding whorls. The protoconch width measure, on the other hand, is the total protoconch width.

9. Number of whorls in protoconch, PRDEGR. Measured in degrees.

c) Widths and Heights

10, 11, 12, 13, 14. Radius of shell (apex to whorl periphery) at whorls 1 through 5, WIDTH1, WIDTH2, WIDTH3, WIDTH4, WIDTH5. Specimens are mounted in clay on a wooden cube, the axis of coiling perpendicular to the base of the microscope. Width measurements are made from the apex to post-protoconch whorls 1 through 5 along a line drawn from apex to whorl periphery at the end of the fifth whorl and projected to a plane perpendicular to the axis of coiling.

15, 16, 17, 18, 19. Height of spire at whorls 1 through 5, HEIGH1, HEIGH2, HEIGH3, HEIGH4, HEIGH5. After the width measures (10–14) are completed, the wooden block is rotated 90° and corresponding height measures made along the same line, this time projected to a plane parallel to the axis of coiling.

d) Angles

20. Angle made by top and bottom of fifth whorl with whorl periphery, angle EFG of Figure 2, PSANGL. The specimen is oriented in a box of magnetite granules so that the whorl periphery (line FGC of Fig. 2) is straight, with point F forming

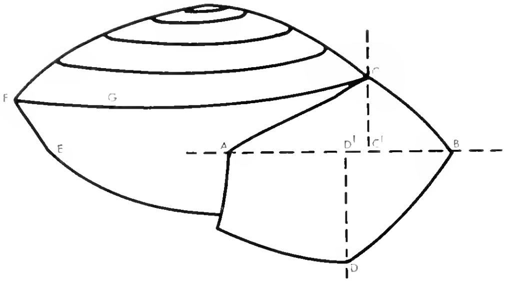


Figure 2. Measurement criteria for apertural variables.

the left extremity of the line segment. The angle is measured by placing the micrometer cross hair in coincidence with line FGC, then rotating it to coincidence with line EF. A protractor is glued to the microscope tube just below the point of contact of eyepiece and tube; a needle is glued to the eyepiece. Rotation of the needle over the protractor gives the angular measurement. I thank Dr. R. L. Batten for teaching me this simple and accurate method.

21. Angle of declination of incremental growth lines at fifth whorl, DANGLE. The specimen is oriented so that a portion of the upper whorl surface at the fifth whorl is as parallel as possible with the base of the microscope. The declination angle is the acute angle made by apertural growth lines with a line drawn tangent to the whorl periphery at the fifth whorl. (Since the incremental striae represent former apertural positions, this method represents a way of standardizing the "aperture inclination," often considered an important variable in describing pulmonate shells.)

2. Measures Derived from Standardized Variables:

22. Ratio of width to height of spire at the end of the fifth whorl, RATIO5. Ratio defined as WIDTH5/HEIGH5, a standardized form ratio.

23. Total size at end of fifth whorl, TSIZE5. Defined as WIDTH5 + HEIGH5. This measure serves as a general size criterion when samples are standardized in a matrix of means.

24. Differential growth ratio, KVALUE. The value of the exponent in the power function (equation of simple allometry)

$$y = bx^k$$

where y is height and x width. When $k > 1$, y is growing faster than x and allometry is said to be positive. Since height increases faster than width in dome-shaped objects, k will always exceed 1 in this study. The higher the value of k, the faster the ratio of raw measures (y/x) rises with increasing size and the stronger the intensity of doming. As will be explained under item 25, however, a high value of k does not necessarily mean that the shell will be relatively high at a standard size near maximum dimensions. That intensity of doming is not a measure of relative height is proven by *Turritella*, rarely excelled in relative height among gastropods, but possessing a triangular cross section and lacking a dome entirely ($k = 1$).

A value of k was calculated for each specimen. The power function provides an accurate approximation of spire geometry from whorl 2 to the end of growth (0.997 is the average correlation coefficient of log y vs. log x). Thus, four points were used in the calculation: (WIDTH2, HEIGH2), (WIDTH3, HEIGH3), (WIDTH4, HEIGH4), and (WIDTH5, HEIGH5).[1] The logarithmic transformation of the power function

$$\log y = \log b + k(\log x)$$

has a linear form in which k is the slope and log b the y intercept. A linear regression program can calculate these parameters when values of the original

[1] The height of the protoconch was subtracted from each of the height measures. The power function applies only to the accretionary part of shell growth and, on this theme, the width and height variables should be rephrased as "perpendicular distance from axis of coiling at nth whorl" and "total height of accretionary part of shell at nth whorl."

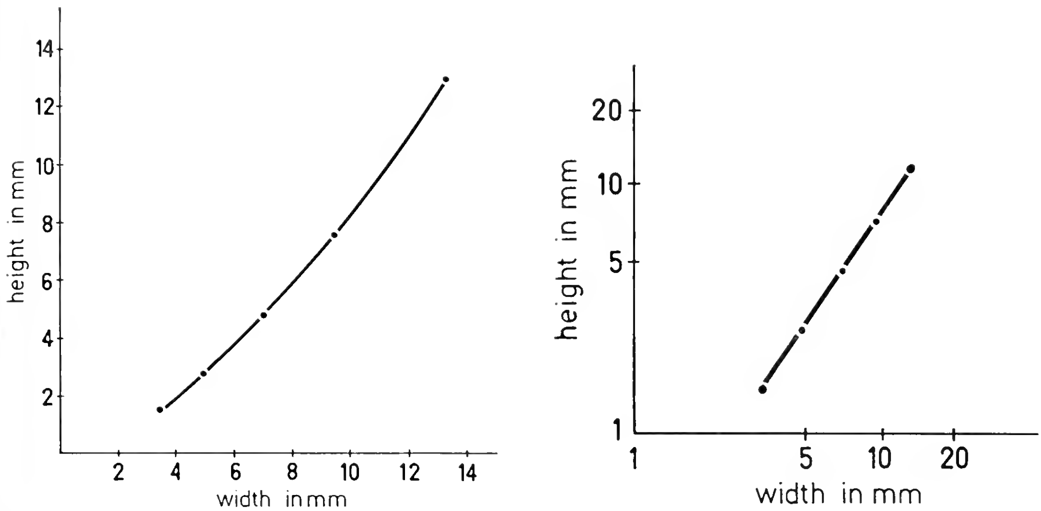


Figure 3. Arithmetic and log-log plotting of width-height pairs for a typical specimen of *P. nelsoni*. 3a (left), arithmetic plot. Curvature represents actual shell geometry as if the cartesian grid were superimposed upon a shell turned upside down so that the apex lies at the origin. 3b (right), logarithmic plot. The straight line indicates that the data are well fit by the power function $y = bx^k$. From Gould (1966a).

data have been transformed to logarithms. k values for more than 1200 snails were computed by DASAN (reduced major axis), and thanks again are due to Dr. T. R. Waller for aid in adapting his program to the peculiarities of this problem. Figure 3 depicts the derivation of this measure in graphical form.

25. Ratio of height to width at the outset of simple allometric growth, INFORM (initial form index). The complete description of a line in a coordinate system requires that two parameters be defined: the slope and the position. The y intercept is usually used as a measure of position. Log b, the y intercept of the log-transformed power function, is an inappropriate measure for two reasons:

a) b is the value of y at x=1. An x value of 1 micrometer unit lies well outside the range of sizes for which the equation is valid (x=30 to 150 units). The y value at an x of 1 is biologically meaningless.

b) b and k are not independent. When, as in this case, x = 1 lies well below the data size range, the correlation of b and k will be strongly negative and this will be a mathematical artifact of the choice of measurement units, for if the units are redefined such that x = 1 now lies above the data size range, the correlation of b and k becomes positive (White and Gould, 1965). That b is a redundant inverse measure of k is demonstrated in Figure 4, depicting the relationship of b and k for 13 samples of *P. cupula*.

Cock (1966) suggests the simple expedient of choosing an x value near the data mean and using ŷ (the predicted value of y at this x) as a measure of position. A more meaningful measure for pulmonates is the value of y at an x at the outset of simple allometric growth. When this is expressed in ratio with x, the measure of position also serves as a form ratio giving the basic shell shape at this point. Since the power function applies from whorl 2 onwards, this ratio is defined as HEIGH2-PRHIGH WIDTH2, the influence of the non-accretionary part of the shell upon its total height again being removed.

The shape of the spire at any point in

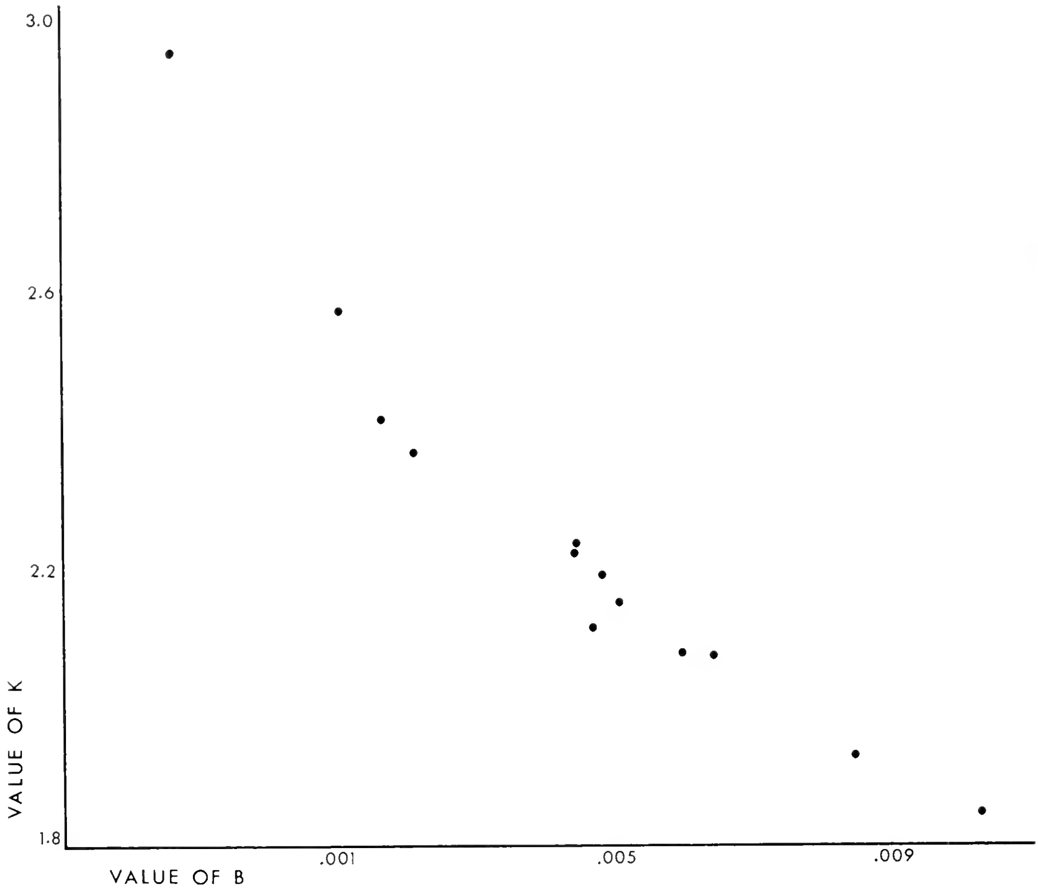


Figure 4. Relationship of b and k among samples of *P. cupula*, illustrating that b is a redundant inverse measure of k for these units of measurement.

ontogeny is a function of three factors: KVALUE, INFORM, and size of the shell at the outset of simple allometric growth (WIDTH2 + HEIGH2):

i) In two shells of identical size and shape at the outset of simple allometric growth, that shell with the higher KVALUE will have a higher and more strongly-domed spire at equal adult sizes because its differential growth of height vs. width was more intense than that of the other shell.

ii) In two shells of identical KVALUE and size at the outset of simple allometric growth, that shell with the higher INFORM will have a higher spire at equal adult sizes because it started simple allometric growth with a higher spire.

iii) In two shells of identical KVALUE and INFORM, that shell which began simple allometric growth at a larger size will, at equal adult sizes, have a lower dome because the same rate of differential increase in height vs. width operated over a smaller range of size.

3. Non-Standardized Variables:

26. Maximum width of the shell, TWIDTH.

27. Maximum height of the shell, THEIGH.

28. Total number of whorls, WHORLS. Measures 26–28 were used as x-values in regressions to obtain standardized values for measures 29–37. By themselves, they do not, of course, appear in the standardized matrices of means.

29. Width of the umbilicus, UMBILC. Predicted values at the standardized size or whorl number for variables 29–37 were obtained by regression.

30. Thickness of the parietal callus, CALLUS.

31. Maximum width of the aperture, APLONG. The apertural measures 31–37 were taken with the shell oriented as follows: perpendicular to the base of the microscope such that the outer whorl periphery (FGC of Figure 2) appears as a line, and rotated dextrally (as the shell grows) to the last point at which the whorl periphery at the aperture (point B) forms the extreme right margin of the field of vision.

32. Maximum height of the aperture, APHIGH.

33. Length of the parietal portion of the inner lip, INNLIP. Line AC of Figure 2.

34. Length of outer lip from posterior extremity of aperture to whorl periphery at aperture, OUTCAR. Line CB, Figure 2.

35. Distance from whorl periphery at aperture to projection of point C upon line AB, UPPOFF. Line C'B, Figure 2.

36. Distance from point A to projection of lowermost point of outer lip upon line AB, LOWOFF. Line AD', Figure 2.

37. Distance from line AB to lowermost point of outer lip, HALFAP. Line D'D, Figure 2.

4. Measures Derived from Non-Standardized Variables:

38. Ratio of total width to total height, WIDIVH. TWIDTH/THEIGH.

39. Total size of shell, HPLUSW. TWIDTH + THEIGH.

40. Relative width of the umbilicus, RELUMS. UMBILC/HPLUSW.

41. Ratio of apertural width to apertural height, ALDIVW. APLONG/APHIGH.

42. Ratio of aperture height to total height, RELSPI (relative height of the spire). APHIGH/THEIGH.

43. Upper aperture eccentricity, UPPECC. UPPOFF/APLONG (i.e., C'B/AB in Figure 2). When UPPECC = 0.5, triangle ACB is isosceles and the upper part of the aperture is said to be non-eccentric. Deviation from 0.5 in either direction increases the eccentricity which may be positive or negative.

44. Lower aperture eccentricity, LOWECC. LOWOFF/APLONG (i.e., AD'/AB in Figure 2). When LOWECC = 0.5, triangle ADB of Figure 2 is isosceles.

IV. THE ONTOGENY OF *POECILOZONITES*

A) Principle

Every measure of shape or color is a function of size in *Poecilozonites.* The ontogenetic relationship between each variable and shell size is allometric.

B) The Ontogeny of Color

The treatment of banding as a simple presence-absence phenomenon in pulmonate studies obscures the fact that it has an ontogeny which may be complex. The coloration of juvenile shells is similar in all species of *P.* (*Poecilozonites*); features which distinguish species and subspecies rarely appear before completion of the second whorl. Deposition of color begins on the last 1/2 whorl of the protoconch as even-sided radial stripes, usually four in number and decreasing in width towards the protoconch termination, covering the entire outer whorl surface from its point of contact with the preceding whorl to the umbilicus. After hatching, the even-sided radial stripes continue for approximately one whorl. Gradually the even-sided borders give way to a characteristic zigzag (flame) pattern. (The etymology of *Poecilozonites*, variegated-banded, refers

to the zigzag pattern of early ontogeny.) Soon afterwards, constrictions begin to form in the flame in areas of the whorl which will not be banded in the adult. It is only at this point that banding features characteristic of species and subspecies become apparent (recalling von Baer's law of the development of special from general characters). The similarity early in ontogeny of shells which will differ markedly in color as adults has been noticed but not emphasized in studies of other pulmonate genera. Pink ground color is dominant to yellow in *Cepaea nemoralis*, but some pinks develop slowly in ontogeny, gradually masking the yellow color of early whorls (Diver, 1929). Owen (1965) distinguished four morphs (one streaked and three pallid) in adults of the African land snail *Limicolaria martensiana*. The distinctive patterns develop gradually during ontogeny. "The polymorphism is most striking in fullgrown snails, while in snails less than 10 mm long it is difficult to distinguish the pallid forms from each other, and in snails less than 5 mm long it is impossible to distinguish any of the color forms" (Owen, 1965: 374).

The constrictions become more and more pronounced and may even become complete, breaking the flame into segments. In the presumptive band regions, meanwhile, the flame segments become wider and begin to approach each other. The formation of the solid band is not, as Pilsbry (1888: 289) believed, a simple matter of flame coalescence, however. The flames do become relatively wider, but interstitial color is also laid down between the flame segments in the presumptive band areas. The formation of the solid band is a result of both processes.

The species of *Poecilozonites* do not exhibit the impressive array of color and band patterns shown by such highly polymorphic genera as *Liguus*, *Partula*, or even *Cepaea*. Band color is invariably chestnut brown and although bands may vary greatly in width and intensity of coloration, their number never exceeds three, and the position of these three is invariant: two on the upper whorl surface (one below the upper periphery, the other just above the lower periphery) and one just below the whorl periphery. In addition, there may be a supplementary wash of color (not a true band, for it lacks a previous flame stage and has no definable borders) between the subperipheral band and the umbilicus.

The order of flame-band transitions is invariant and occurs, so to speak, from the bottom up. The subperipheral band always forms first, the band above the lower whorl periphery next and the uppermost band last. Moreover, all the bands continue to increase in relative with during ontogeny, the uppermost band doing so fastest of all. If growth continues sufficiently, the bands fuse.

I have adopted a coding system for banding patterns based upon that used by students of *Cepaea*. Starting from the upper whorl periphery, the uppermost band is 1, the band above the lower periphery 2, the subperipheral band 3, and the supplementary color wash above the umbilicus S (for it is not a true band). If the flame-band transition has not occurred by the fifth whorl, a superscript "f" is added after the number of the band. If, as in some forms of *P. cupula*, a band is less than 1/10 the whorl width (at which point it would customarily be called a "line" rather than a band), a superscript "n" is added after the number of the band. If a band is completely absent at the fifth whorl, its position is recorded as 0. (In *Cepaea*, 0 implies that no aspect of the band ever forms. This never happens in *Poecilozonites*. Flame predecessors of the band always appear on the early whorls, but in some morphs, the flames, rather than increasing in strength, become gradually weaker and are finally effaced. When the supplementary color wash is absent, no 0 is recorded because it has no flame stage.) Bands which are fused by the end

of the fifth whorl are enclosed in parentheses. Thus, when a specimen has three discrete bands and a supplementary wash at the end of the fifth whorl, it is recorded as 123S (a common pattern for *P. bermudensis zonatus*). If the upper band has yet to form (flames being present), the second band is less than 1/10 the whorl width, the third band is normal, and the supplementary wash absent, the shell is coded 1^f2^n3 (one of the morphs of *P. cupula cupuloides;* another morph of the same subspecies lacks all but the upper band and is coded 100).

In conclusion, the ontogeny of banding in *Poecilozonites* is marked by a gradual and continual increase in the intensity of coloration. This increase is manifested in two ways: by the transition from intermittent flammules to a solid band and by the increase in relative width of the bands, often resulting in their eventual fusion.

C) *The Ontogeny of Shape*

The complexity of allometric trends in the ontogeny of *Poecilozonites* results primarily from the interplay of two factors:

1. "Nucleating" influence of the protoconch: The protoconch of *Poecilozonites* forms within the egg. The adaptive significance of its shape is probably related to functional and mechanical pressures not relevant to later accretionary growth. Its basic shape, therefore, may be expected to bear little relation to those shapes produced by developmental trends operating during the post-embryonic life. Yet the protoconch is a nucleus about which the post-embryonic shell must form and, like the cubic nucleus of a spherical concretion, its influence will not be overcome until the shell has built out a fair distance from it.

Two features of protoconch form are especially relevant to its nucleating influence (Plate 3, Figs. 6–7):

a) It has a very low spire.

b) The aperture is high and narrow.

Upper and lower apertural eccentricities (see Chapter 3, section C, items 43 and 44) are very strong (LOWECC and UPPECC measuring close to 0.0). I suspect that mechanical limitations of space within the egg largely determine the protoconch's quadrate, blocklike shape.

2. Influence of doming in post-embryonic growth: Post-embryonic growth begins with a strong increase in relative width, gradually converting the quadrate protoconch to the wide, low shape characteristic of early whorls. As growth proceeds, the effects of doming become dominant; growth in height exceeds that of width, height of the spire increases relative to height of the aperture, and the shell becomes relatively higher. Three stages in the ontogeny of the aperture and spire may be defined:

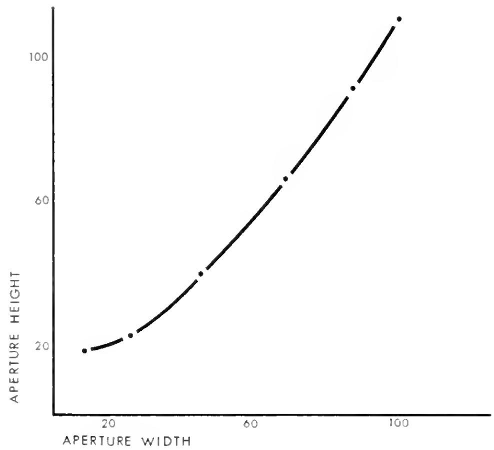
a) protoconch: low spire, relatively high aperture, low width/height

b) intermediate: low spire, relatively wide aperture, high width/height

c) maximum size: high spire, relatively high aperture, low width/height.

The similarity of protoconch and adult in some measures of gross morphology does not indicate any functional similarity, since the resemblance is attained in different ways. (A relatively high aperture determines the low width/height ratio of the protoconch; the same low ratio in a large shell is mainly a function of spire height.) The loss and reacquisition of certain shapes do, however, lead to complex bivariate trends in ontogeny. Take, for example, the relationship of aperture length and aperture height[1]. Figure 5 depicts this relationship for an average specimen of *P. bermudensis zonatus.* The concave upward trend of the curve reflects the doming influence in post-

[1] This relationship should be studied longitudinally (as it develops in single specimens) not cross-sectionally (inferred from mass curves in which each point is a specimen). This can be done by measuring a large specimen and then carefully breaking off a section at a time to obtain points for earlier ontogeny. Since the incremental striae represent former apertural positions, the shell can be trimmed back quite precisely to any of its former apertures.



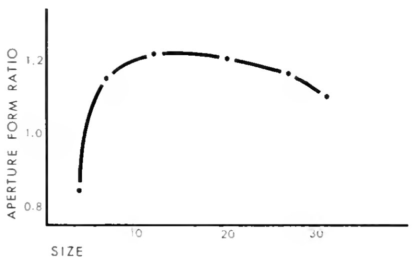


Figure 5. The determinants of ontogenetic allometry: "nucleating influence" of protoconch and doming in post-protoconch ontogeny. Longitudinal data based on a single *P. bermudensis zonatus* from Government Quarry. Pattern completely general for the genus. 5a (above) in micrometer units at 1 unit = .0727 mm. 5b (below) in mm.

protoconch growth; the increase of height relative to width is evident in the form of the curve. If this curve had its origin at (0,0), the ontogeny of the apertural form ratio would be simple: the relative height of the aperture would increase in an even fashion. Due to the nucleating influence of the protoconch, however, the curve does not begin at (0,0) and the ontogeny of the form ratio is complex (Fig. 5b). There is, at first, a sharp *decrease* in relative height as the initial flattened increments are accreted onto the high protoconch. This decrease is not reversed until the third whorl, when the doming trend bcomes dominant and relative height of the aperture begins to increase.

In the last chapter, the variables of this study were grouped into four categories: standardized, derived standardized, non-standardized, and derived non-standardized. Variables in the first two categories have no ontogeny, though the biological features that they measure may undergo allometric growth. (Although the whorl number of a flame-band transition is a single point with no ontogeny, the transition itself reflects a trend towards increasing intensity of coloration. Although the differential growth ratio is constant for a shell, its magnitude measures the most important feature of post-protoconch allometry — the intensity of doming.)

A variable by variable description of allometry in the ontogeny of non-standardized variables and ratios is presented below:

a) UMBILC: The width of the umbilicus increases rather rapidly to a maximum size, after which it remains constant or, in high-spired shells, decreases by constriction (Fig. 6).

b) RELUMS: The relative width of the umbilicus increases slightly, then decreases evenly throughout growth. RELUMS is a conventional pulmonate measure (used by Pilsbry in his taxonomic studies of *Poecilozonites*), and its use is often justified as a means of obtaining comparisons that will be independent of size. It is ironic that just the opposite effect results from its use in *Poecilozonites*. The raw

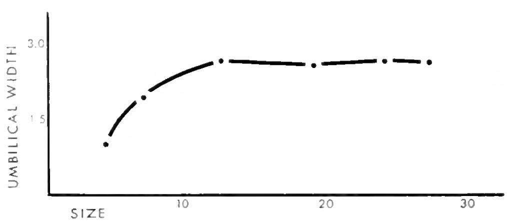


Figure 6. Typical ontogenetic development of umbilical width in *P. (Poecilozonites)*. Early rapid increase followed by stability. In mm.

measure UMBILC rapidly reaches a maximum dimension which usually remains invariant during growth. When a constant is used as the numerator in a ratio with size, variation of the ratio with growth will be completely due to increase in its denominator, and the stated purpose of the ratio is confounded. For later ontogeny at least, UMBILC itself is the size-independent measure.

c) CALLUS: The parietal callus is absent in *P. cupula*. In *P. nelsoni* and *P. bermudensis zonatus*, it rarely forms until the fourth whorl, thereafter increasing gradually in relative thickness. Complexity is introduced when callus thickening continues during a growth pause; a snail which estivated for several months at whorl 5 and then began to grow rapidly will show an initial decrease followed by the usual gradual increase.

d) WIDIVH: The relative width of the shell increases until the protoconch's influence is overcome; then it decreases gradually (doming effect of post-protoconch ontogeny).

e) ALDIVW: The relative width of the aperture increases sharply at first, then more slowly until the nucleating influence is overcome. Thereafter, as a result of differential increase in shell height measures, it decreases slowly.

f) RELSPI: The spire of the protoconch is virtually flat. Throughout postembryonic growth, height of the spire increases relative to height of the aperture and RELSPI (aperture height total height) undergoes a regular decrease throughout ontogeny.

g) UPPECC: Increases sharply at first as the flattened early whorls are added to the quadrate protoconch. Thereafter, a slight decrease occurs as the aperture increases slowly in relative height.

h) LOWECC: With RELSPI, the only ratio measure displaying an unreversed trend in ontogeny. Lower eccentricity of the protoconch is 0.0; it increases slowly during ontogeny up to the fourth whorl. During formation of the fifth whorl, a large

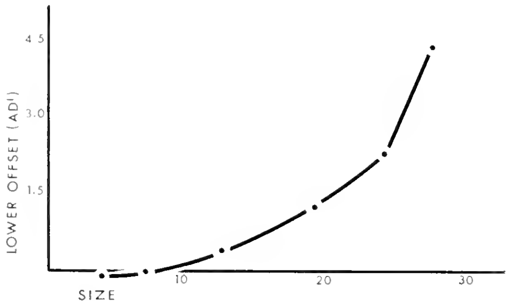


Figure 7. Typical ontogenetic development of lower apertural eccentricity: slow increase followed by rapid increase late in ontogeny. Figs. 5–7 based on the same specimen, which displays patterns completely general for the genus. In mm.

and rapid expansion occurs (Fig. 7). LOWECC is the only measure of shape which consistently undergoes its most rapid modification during a late stage of ontogeny.

With minor exceptions (*P. cupula* lacks a callus; the umbilicus becomes constricted in high-spired forms), the same ontogenetic trends apply to all species of *P.* (*Poecilozonites*).

V. INTERRELATIONSHIPS OF VARIABLES

> It seemed to the writers, as it has to others, that character changes occurring in evolution of species could not be considered to be independent of each other and that studies which did not consider this dependency ignored a significant aspect of change.
>
> Olson and Miller, 1958: 1

A) *Factor Analysis*

A matrix of distance measures, itself a major reduction of raw data, is still sufficiently vast in scope to mask patterns of interrelation among many variables. Some technique must be applied to abstract a simpler pattern from the matrix.

Factor analysis, the technique used here, resolves a set of samples (Q mode) or variables (R mode) into a far smaller number of reference axes. Each sample or variable is depicted as a vector; vectors radiate from a common point and the

cosine of the angle between any two is a measure of their correlation. Thus, perfectly correlated vectors will overlap (cosine of $0° = 1$), while orthogonality (right angle separation) reflects a correlation of zero. Reference axes are constructed within the vector set; various schemes for positioning these axes can be used in the attempt to reach meaningful solutions. In the principal components solution, the first reference axis is that which resolves the most information possible for any single axis. Since the high positive correlation between most body parts in ontogeny is due to the common factor of increasing body size, this axis has been widely interpreted as a general growth factor in R-mode analysis (Teissier, 1948, 1955; Matsuda and Rohlf, 1961; Jolicoeur and Mosimann, 1960; Ouellette and Quadri, 1966). When an orthogonal criterion is maintained for reference axes (mutual orthogonality = mutual independence), other axes are constrained to lie perpendicular to the first principal component. These axes may be mathematical abstractions having no special claim to biological interpretability, and the method has been attacked from this standpoint. If attempts are made to provide the reference axis itself with some biological meaning, this objection is potentially valid. But the axes can also be considered merely as references for defining the positions of vectors within the set. It is in this latter sense that factor analysis is comparable to other multivariate clustering techniques. Thus Boyce (1964), in a Q-mode study of hominoids, used the principal components axes as coordinate systems for a set of two-dimensional slices through the vector swarm. Plots of vector positions on a series of such slices provide a pictorial representation of sample interrelationships that is, in many ways, superior to hierarchical dendrograms (for these give no direct measure of relative distances among individual samples in different clusters). I have used factor axes in this second sense—as references about which vectors may cluster. It is the clustering that demands interpretation. My rationale for rotating the reference axes to positions in coincidence with actual vectors (see next paragraph) is not that the axes then claim greater interpretability, but that they will be more likely to lie near (and therefore serve as references for) groups of associated vectors.

In the varimax solution, reference axes keep their positions relative to each other, but the entire system is rotated within the set of vectors so that the axes fall nearest those vectors which lie at geometric extremes of the vector set. In Q-mode plots discussed in Chapters 6–10, varimax axes are used for coordinate systems. In the oblique solution, used throughout this chapter, the criterion of mutual orthogonality is abandoned and actual vectors lying at extreme positions in the vector swarm are used as reference axes. The final step of each analysis is a matrix whose elements represent the projection of each variable on each reference axis. Each variable is grouped with the reference axis upon which its vector most strongly projects. A reference axis (itself a variable) and its associated variables form a set which may delimit a functional complex of interdependent measures mirroring a common causal factor. Factor analyses were performed on the Columbia University IBM 7094 using Manson and Imbrie's (1964) program COVAP. See Manson and Imbrie (1964), Imbrie and Van Andel (1964), and Gould (1967) for more information on this program.

B) Interrelationships of Variables: Eight Reference Axes

As an example, I shall discuss the oblique projection matrix of a particularly favorable sample. COVAP does not handle matrices with missing data; since approximation was rejected as a source of bias, variables which could not be measured in all specimens were omitted from the analyses. These Government Quarry snails (locality

5) pack a Shore Hills fissure in such abundance that local quarrymen call this area "the graveyard." Preservation is excellent and all variables (with the exception of COLOR3) could be measured in all specimens. Since factor analysis assumes linear relationships among variables, the entire size range cannot be used (see Chapter 4 on complex relationships caused by the protoconch's "nucleating" influence upon early whorls). If the smallest specimens are safely beyond the point of zero slope for non-monotonic relationships, then the linear approximation is sufficiently accurate. The 25 Government Quarry specimens, varying from 23.2 to 37.8 mm in HPLUSW, range in whorl number from 5 to 6⅛; 45 variables were resolved into 8 reference axes which accounted for 91.3 per cent of the total information.

Interpretation of variable clusters (Table 3):

Axis 1: All non-standardized raw measures with the exception of UMBILC, CALLUS, and UPPOFF, sort with the first axis. In addition, two strongly size-dependent ratios—LOWECC and RELSPI—have their highest projections on this axis (the projection of RELSPI is negative, since its value decreases with increasing size). The biological interpretation of this association is clear: it includes all those measures most strongly correlated with specimen size and is therefore termed the size cluster.

Axis 2: All the standardized measures of early whorl heights sort with this axis. INFORM (HEIGH2-PRHIGH/WIDTH2) includes measures of this group as its numerator; KVALUE projects negatively because high intensity of doming implies a flattened apex and correspondingly low early heights. The association of these variables produces a shell which is relatively high early in ontogeny and, consequently, not strongly domed.

Axis 3: A heterogeneous group of variables sharing the common attribute of tending to produce a relatively wide shell. Although it is a non-standardized variable, UMBILC does not sort with the first axis, because its value is independent of size in the range of this analysis. The form ratio of the shell is the main determinant of its variability; a relatively wide shell mechanically produces a wide umbilicus. WIDIVH, although correlated with size, is in this case more strongly influenced by shape factors tending to produce a relatively wide shell. RELUMS is a redundant measure sorting either with its numerator or denominator. A relatively wide shell tends to be low at late whorl numbers (negative projections of HEIGH5 and HEIGH4), to have a sharp periphery (low PSANGL) and, by definition, a low height/width ratio at standardized whorl numbers.[1]

Axis 4: Standarized widths of later whorls. TSIZE5 includes WIDTH5 as part of its measure. The inclusion of DANGLE, if biologically significant, implies that a shell which is large at a late whorl has a low apertural inclination.

Axis 5: Protoconch width: The inclusion of early whorl widths indicates the extent to which their value is not independent of the protoconch. As more whorls are added, the protoconch width makes up progressively less of the total width and its influence is overcome, usually by the fourth whorl.

Axis 6: LI/CAR (INNLIP/OUTCAR), the reference for this group, is not included in the listing of Chapter 3 because it was found to be a redundant inverse measure of UPPECC. All variables sorting with this axis are related to the upper part of the outer lip of the aperture. OUTCAR,

[1] As given in Chapter 3, RATIO5 = WIDTH5 - HEIGH5. This will be its definition in the matrices of means. In the factor analyses described in this chapter, its value is inverted (height - width). I regret the confusion, but took this expedient because the regression program DASAN printed out height width ratios at each whorl for each specimen (giving both INFORM and RATIO5).

TABLE 3. OBLIQUE PROJECTION MATRIX, GOVERNMENT QUARRY SAMPLE

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8
WHORLS	1.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
LOWECC	0.906	−0.088	0.023	0.731	0.140	0.469	0.236	0.497
LOWOFF	0.895	−0.061	0.086	0.770	0.220	0.408	0.097	0.422
INNLIP	0.771	−0.002	0.009	0.570	0.382	0.437	−0.374	−0.260
TWIDTH	0.706	0.011	0.193	0.529	0.318	0.043	−0.305	−0.113
HPLUSW	0.706	−0.009	0.013	0.399	0.330	−0.010	−0.302	−0.223
APWIDT	0.697	0.037	0.165	0.583	0.305	0.040	−0.291	−0.052
THEIGH	0.663	−0.035	−0.232	0.202	0.329	−0.084	−0.280	−0.362
APHIGH	0.587	−0.029	−0.072	0.464	0.350	0.036	−0.379	−0.391
HALFAP	0.516	0.015	0.051	0.499	0.369	−0.114	−0.317	−0.226
OUTCAR	0.515	−0.002	0.011	0.318	0.252	−0.380	−0.263	−0.178
RELSPI	−0.641	0.048	0.456	0.344	−0.073	0.230	−0.086	0.101
TOTECC	−0.803	0.043	−0.043	−0.657	−0.099	−0.084	−0.210	−0.464
HEIGH1	0.000	1.000	0.000	0.000	0.000	0.000	0.000	0.000
HEIGH2	0.054	0.922	−0.243	−0.067	0.058	−0.067	0.004	−0.341
PRHIGH	0.164	0.911	0.220	0.247	−0.262	−0.084	0.282	0.470
INFORM	0.020	0.827	−0.388	−0.226	−0.063	−0.040	−0.009	−0.523
HEIGH3	−0.130	0.724	−0.501	0.008	0.109	−0.294	0.048	−0.429
KVALUE	−0.153	−0.962	−0.060	−0.116	0.331	−0.399	0.154	0.292
UMBILC	0.000	0.000	1.000	0.000	0.000	0.000	0.000	0.000
WIDIVH	−0.337	0.116	0.813	0.351	−0.173	0.213	0.073	0.576
RELUMS	−0.531	0.025	0.660	−0.316	−0.207	−0.003	0.207	0.171
HEIGH5	−0.181	0.076	−0.639	0.491	0.466	−0.368	−0.274	−0.548
HEIGH4	−0.252	0.357	−0.710	0.112	0.435	−0.424	−0.116	−0.589
PSANGL	−0.174	−0.435	−0.898	−0.435	0.087	−0.288	0.101	−0.703
RATIO5	−0.171	0.037	−0.925	−0.129	0.160	−0.604	0.095	−0.446
DANGLE	0.000	0.000	0.000	1.000	0.000	0.000	0.000	0.000
WIDTH5	−0.046	−0.062	0.269	0.846	0.553	0.259	−0.575	−0.324
TSIZE5	−0.128	0.004	−0.190	0.788	0.595	−0.046	−0.503	−0.502
WIDTH4	0.001	−0.166	0.216	0.785	0.643	0.245	−0.467	−0.273
PRWIDT	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.000
WIDTH1	0.031	−0.057	0.093	−0.107	0.993	−0.065	−0.127	−0.315
WIDTH2	−0.004	−0.157	0.132	0.220	0.957	−0.018	−0.260	−0.284
WIDTH3	−0.117	−0.170	0.164	0.469	0.911	0.101	−0.426	−0.305
LI CAR	0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000
UPPOFF	0.447	0.070	0.133	0.349	0.145	−0.531	−0.152	0.048
UPPECC	0.111	0.088	0.062	0.112	−0.051	−0.928	0.027	0.128
COLOR4	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000
COLOR5	0.132	−0.098	−0.109	−0.103	−0.032	−0.056	0.894	−0.254
PRDEGR	0.236	−0.056	−0.088	−0.014	0.495	0.092	0.525	0.071
LOWCOL	0.093	−0.052	−0.180	0.233	−0.243	−0.347	0.383	−0.303
ONSELO	−0.393	−0.159	−0.071	−0.197	0.624	−0.285	−0.703	0.373
ONSEUP	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000
ALDIVW	0.397	0.194	0.670	0.362	−0.130	−0.016	0.225	0.870
CALLUS	0.258	0.080	−0.573	−0.011	0.109	−0.137	−0.463	−0.729

another variable in morphological proximity to these, sorts with the size axis (though more weakly than any other variable of that group), but also projects fairly strongly on axis 6.

Axis 7: Color: All but one of the color measures sort with axis 7 as a discrete group. Band onsets (ONSELO) correlate negatively with variables measuring the relative width of color bands. ONSELO is the whorl number of a flame-band transition; the transition occurs at a high whorl number if coloration is weak. The weak sorting of PRDEGR with this axis is probably spurious: it projects almost as highly upon the PRWIDT axis.

Axis 8: A difficult axis to interpret. The association of a relatively wide aperture and a weak callus could record the effects of size (both are characteristic of small specimens). The inclusion of ONSEUP is confusing; weak color is also a feature of small specimens, but ONSEUP is a standardized variable and cannot directly reflect size. CALLUS might be expected to sort with the first axis, but variation in its thickness due to growth pauses (see Chapter 4) is sufficient to mask the weaker correlation with size. The callus is already fairly well developed by the fifth whorl; if a wider size range were used in this analysis, the primary correlation with size would assert itself. The eighth axis accounts for only a small part of the total information and its associations are probably not significant. Nonetheless, the use of many axes may define weak associations which are otherwise overwhelmed by such dominant factors as size.

The status of ALDIVW illustrates the caution with which data of this type must be approached. In longitudinal studies ALDIVW always declines during ontogeny, although that decline is slight. Here, however, the projection of ALDIVW on the size axis is weak but *positive*. The data used for these analysis fall into the "mixed cross-sectional" category of Cock (1966). One set of measures is made per specimen and no age criteria are available. "Variation in size and shape at a fixed age, and variation due to age are inseparably confounded" (Cock, 1966: 236); ontogeny may be poorly represented, or even misrepresented, by such data. Figure 8 depicts the relationship of ALDIVW vs HPLUSW for 46 specimens from Government Quarry. If the entire size range is considered and the circled points ignored, the mixed cross-sectional trend faithfully represents the negative correlation of individual ontogeny. When the size range is compressed, the influence of the static component (that due to variation at a given size) increases and, in this case, actually reverses the correlation. The largest specimens of most *Poecilozonites* samples tend to be relatively wide. When the circled points (7 of the 10 largest specimens) are included and only those specimens reaching 5 whorls considered, the correlation becomes slightly, though insignificantly, positive.

In conclusion:

a) Absolute size is the dominant factor in relationships among non-standardized variables and the measures derived from them. Only two complexes of non-standardized variables fail to associate with the size cluster—those dealing with relative width of the shell and the upper part of the outer lip of the aperture.

b) Of standardized variables and their derived measures, the following is noted:

i) Heights and widths sort separately. There is, moreover, a tendency for their assortment into four clusters: early heights, late heights, early widths and late widths In this analysis

1) early heights are associated with measures of doming intensity.

2) late heights group most strongly (negatively) with variables producing a shell of high relative width.

3) early widths (the value of which includes the protoconch width) sort with the protoconch width.

4) the later widths constitute a separate assemblage.

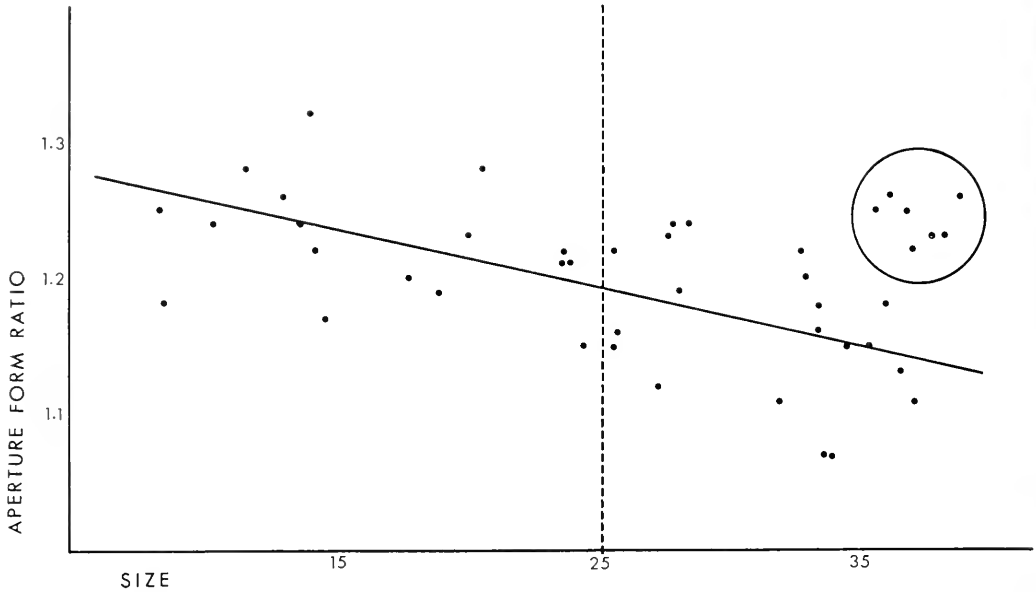


Figure 8. Apertural form ratio vs. shell size for all measured specimens of the Government Quarry sample of *P. bermudensis zonatus*. Consult text for interpretation of regression and circled points. Dotted line separates specimens of five whorls or more from specimens of smaller whorl number. The factor analysis described in text considered only those specimens reaching five whorls.

ii) Color measures sort as a discrete cluster.

C) *Hierarchy of Interdependence: Successive Reduction of Axes*

The 8-axis scheme is a horizontal transect through a hierarchical structure of interrelationships. It displays a set of groupings at a pre-set level of resolution but gives little information on the relative independence of clusters. Taking non-standardized variables, for example, we find that size exerts a controlling influence. A most important facet of the search for explanation involves a vertical question not answered in a single analysis: What is the hierarchy of size dependence? What groups of non-standardized variables are most strongly size-independent and why? "Most structures tend to contribute to total body size by increasing in dimensions during ontogeny. It is of interest to determine whether this influence is dominant, overshadowing the effects of function and other possible factors" (Olson and Miller, 1958:86). The authors of this passage have used their techniques of "morphological integration" to approach such questions. By successively lowering the level of correlation defining basic groups, clusters which were discrete at higher levels merge in gradual sequence. In the frog *Rana pipiens*, for example, forelimb and hindlimb complexes are separate at the highest level used; at lower levels these unite to form a single association of locomotory measures. The vertical dimension is obtained in a different and only roughly analogous way in this study—by a successive reduction of reference axes. The sequential elimination of axes accounting for the least amount of information causes groups to merge in patterns that reflect the relative importance of various determinants of shell form. Successive reductions to one factor were performed on the Government Quarry sample with the following results:

7 axes: Axis 8 of the previous analysis

is dispersed. CALLUS and ALDIVW join the "relatively wide shell" variables of axis 3. A relatively wide shell tends to have a relatively wide aperture and a weak callus. ONSEUP now groups (negatively) with the "wide at later whorls" axis 4, but its projection on the "color" axis 7 is only slightly weaker. RELUMS has moved to the size cluster (axis 1). HEIGH4 now correlates most strongly with heights of earlier whorls (axis 2); HEIGH5 sorts with WIDTH5. WIDTH2 and WIDTH3 move to axis 4, leaving WIDTH1 to sort with the protoconch width. PRDEGR now groups with PRWIDT. Two of the color measures (COLOR4 and COLOR5) are incorporated into the protoconch width group. The seven clusters are interpretable and, judging from the minimal amount of subsequent shifting, quite stable. As values of the variables increase, the seven clusters produce:

1. a large shell
2. high early heights and low doming intensity
3. a relatively wide shell
4. wide (and large) shell at later whorls
5. a large protoconch and strong coloration
6. a large outer apertural lip
7. a strongly colored shell

6 axes: The color group is eliminated and its members allocated to the third axis. In addition, COLOR5 shifts to the third axis, leaving COLOR4 with the protoconch width group. The signs of vector projections on axis 3 are reversed. The same variables are involved, but increase in their values now produces a relatively high shell. More generally, the third axis variables are a group determining the form ratio of the shell. They are related more strongly to shape at a given size than to size itself. (Since shape is a function of size, this distinction may seem unwarranted, but most of these variables are standardized and unrelated to size.)

1. a large shell
2. high early heights and low doming intensity
3. a relatively high and strongly colored shell
4. wide (and large) shell at later whorls
5. a large protoconch and strong coloration
6. a large outer apertural lip

5 axes: The last discrete group of non-standardized variables is incorporated in the first (size) axis. CALLUS and UMBILC, which show no correlation with size in this sample, are now the only non-standardized raw variables not grouped with the first axis. In addition, two non-standardized ratios (the shell and apertural form ratios WIDIVH and ALDIVW) sort with the "shape" axis 3.

4 axes: The two width clusters (whose references were, respectively, protoconch width and width at the fifth whorl) are combined into one set. COLOR4 joins the third axis cluster and all color measures are now aligned in this group. Four axes account for 75.3 per cent of the total information.

3 axes: The standardized widths are absorbed into the first axis assemblage. HEIGH4 and HEIGH5 now sort with the "relatively high shell" axis 3.

2 axes: All measures of standardized and relative height are conjoined in a second axis cluster. Non-standardized size measures and standardized widths sort with the first axis. Two axes account for 59.1 per cent of the total information.

1 axis: COVAP cannot rotate a single axis (rotation would serve little purpose in any case). This axis is the first principal component, which is, in this case, a general size factor accounting for 42.0 per cent of the total information. If each variable is ranked according to the percentage of its information accounted for by this axis, a chart of relative size dependency results. Two such charts are presented in Table 4, one for Government Quarry, the other for 29 specimens of *P. bermudensis fasolti*

TABLE 4. PERCENTAGE OF INFORMATION ACCOUNTED FOR BY FIRST PRINCIPAL COMPONENT (GENERAL SIZE FACTOR). Non-standardized raw variables indicated (*), non-standardized ratios as (#).

A) *Government Quarry Sample*

*HPLUSW	0.905	#RELSPI	0.350
*THEIGH	0.899	*CALLUS	0.334
*APHIGH	0.889	#LI/CAR	0.332
*HALFAP	0.877	RATIO5	0.312
*OUTCAR	0.853	PRWIDT	0.311
*TWIDTH	0.838	LOWCOL	0.293
*APWIDT	0.829	DANGLE	0.292
*INNLIP	0.739	PRDEGR	0.286
*UPPOFF	0.694	WIDTH5	0.281
HEIGH5	0.683	ONSEUP	0.222
#TOTECC	0.670	COLOR5	0.220
*LOWOFF	0.656	HEIGH3	0.154
TSIZE5	0.610	COLOR4	0.099
#RELUMS	0.581	PSANGL	0.085
*WHORLS	0.580	ONSELO	0.081
#LOWECC	0.534	HEIGH2	0.064
WIDTH2	0.491	KVALUE	0.025
WIDTH1	0.431	INGRIN	0.023
HEIGH4	0.431	*UMBILC	0.008
WIDTH3	0.372	#ALDIVW	0.001
#WIDIVH	0.369	HEIGH1	0.000
WIDTH4	0.366	PRHIGH	0.000
#UPPECC	0.353		

B) *Tom Moore's Cave Sample,* P. bermudensis fasolti

*HPLUSW	0.973	WIDTH3	0.167
*TWIDTH	0.970	WIDTH4	0.141
*APLONG	0.963	WIDTH2	0.115
*THEIGH	0.954	PRDEGR	0.082
*INNLIP	0.934	TSIZE4	0.080
*APHIGH	0.897	*UMBILC	0.045
#RELUMS	0.869	PRHIGH	0.022
*WHORLS	0.813	KVALUE	0.011
*OUTCAR	0.806	INGRIN	0.011
#WIDIVH	0.804	HEIGH3	0.010
#LOWECC	0.470	HEIGH4	0.008
#RELSPI	0.450	RATIO4	0.007
#UPPECC	0.318	HEIGH2	0.005
PRWIDT	0.262	#ALDIVW	0.004
WIDTH1	0.244	HEIGH1	0.003

from locality 53. The large size range (16.5–37.7 mm HPLUSW) of this latter sample is especially conducive to the assessment of size dependency.

TABLE 5. CORRELATION MATRICES OF STANDARDIZED WIDTHS AND HEIGHTS

A) *Government Quarry Sample,* P. bermudensis zonatus

	HEIGH1	HEIGH2	HEIGH3	HEIGH4	HEIGH5
WIDTH1	−0.040	0.107	0.160	0.441	0.529
WIDTH2	−0.212	−0.070	0.027	0.378	0.591
WIDTH3	−0.290	−0.193	−0.091	0.279	0.550
WIDTH4	−0.353	−0.270	−0.171	0.177	0.523
WIDTH5	−0.318	−0.268	−0.171	0.135	0.474

B) *South Shore Local Population,* P. cupula cupula

	HEIGH1	HEIGH2	HEIGH3	HEIGH4	HEIGH5
WIDTH1	0.211	0.368	0.505	0.540	0.550
WIDTH2	0.134	0.296	0.435	0.519	0.598
WIDTH3	0.099	0.257	0.378	0.519	0.652
WIDTH4	0.073	0.200	0.296	0.394	0.578
WIDTH5	0.071	0.183	0.214	0.248	0.334

From the successive reduction of factor axes, I conclude:

a) The strong relative independence of a group of non-standardized variables related to the upper part of the outer apertural lip is confirmed. These are not incorporated into the size grouping until axes are reduced to 5. Of the non-standardized variables and their derivatives, only UMBILC and ALDIVW are virtually size-independent (the first principal component accounts for less than 0.05 per cent of their information in both samples of Table 4). In the case of ALDIVW, this lack of correlation with size is an artifact of the use of mixed cross-sectional data to approximate ontogeny.

b) Of all standardized variables, early heights are most consistently independent of size; protoconch and whorl widths display a small size contingency. This situation is clarified in Table 5, which presents matrices of correlation coefficients among standardized widths and heights for the Government Quarry sample and for a collection of 35 specimens of *P. cupula cupula*

from locality 41.[1] The widths of early whorls correlate strongly and positively with heights of later whorls (r of WIDTH1 through WIDTH4 with HEIGH5 is significant at the 1 per cent level in all cases). Early whorl heights, on the other hand, show no correlation (usually insignificantly negative) with later widths. (The correlation of widths with widths and heights with heights is not shown, but is always positive.) Thus, a shell which is *wide* at an early whorl tends to be *large* at a later whorl, while a shell which is *high* at an early whorl tends to be *relatively high but not necessarily large* at a later whorl. If each shell has an equal chance of reaching the same final whorl number, then a shell which is large at the end of the first whorl is likely to be absolutely large at its terminal size. Thus, early widths will bear some relationship to absolute size, while early heights will not.

c) When the discrete color cluster is dispersed by elimination of its axis, the color measures group either with variables related to a relatively high shell or to wide early widths. The previous discussion provides an interpretation for this tendency. Wide early widths imply a relatively high shell at large sizes; such a shell, it would appear, also tends to be strongly colored. With rare exceptions (visual predation of *Cepaea* by thrushes), the adaptive significance of molluscan color patterns is unknown. The discovery of morphological features to which these patterns relate opens the possibility of interpreting evolutionary changes in coloration as pleiotropic responses allied to morphological modifications.

D) Consistency of Results in Other Samples

In order to determine the generality of conclusions based upon the Government Quarry sample, analyses were performed on 10 additional collections of *P. bermudensis* and *P. cupula* (8 reference axes in each case). Since size exerts a controlling influence upon most non-standardized variables, samples differing in size range were selected. As the size range decreases, the percentage of variation attributable to size in non-standardized measures diminishes and relationships previously swamped by the primary factor of size become apparent.[2] Results of the 10 analyses are presented as a table (Table 6) giving the following information for each sample: number of specimens, number of variables, percentage of total information accounted for by 8 axes, range of specimen size (largest − smallest/largest), percentage of variables grouping with the "size" reference axis, and the interpretation of each reference axis cluster. These interpretations follow:

1. Associations attributable to size differences among specimens: S if one single cluster, WS and HS if widths of non-standardized variables sort separately from heights.

2. Assemblages of non-standardized apertural variables; UAP for measures of the upper part of the outer apertural lip (OUTCAR, UPPOFF, UPPECC). LAP for measures of the subperipheral portion of the outer lip (LOWOFF, LOWECC).

3. Other aggregates, including non-standardized variables:

a) FR (form ratio), a heterogeneous group of variables related to the width/height ratio of the shell at the fifth whorl. FR may include the following: raw non-standardized (UMBILC, since a relatively wide shell has an absolutely wide umbilicus), derived non-standardized (WIDIVH, ALDIVW, and RELSPI, the last because a relatively wide shell has a relatively low spire), raw standardized (PSANGL), and derived standardized (RATIO5).

b) U, the umbilicus, which usually groups in FR, may sort independently.

[1] The patterns are representative of 10 other such matrices and seem to be completely general.

[2] The factoring of partial correlation matrices (with the effects of size removed) would probably be a better approach to this problem.

TABLE 6. INTERPRETATION OF FACTOR AXIS GROUPINGS FOR 11 SAMPLES OF *P.* (*POECILOZONITES*). Interpretation of columns as follows: 1, subspecies name and locality number of sample; 2, N the number of specimens in the sample; 3, V the number of measured variables; 4, % the percentage of total information accounted for by 8 factors; 5, R the range of specimen size within the sample (largest – smallest/largest); 6, S the percentage of variables grouping with the general size factor; 7–23, column headings are the interpretation of the reference axis (explained in text pp. 441–443), the recorded figure is the number of the reference axis whose accompanying cluster of variables bears the interpretation of the column heading.

Sample	N	V	%	R	S	S	WS	HS	PRW	LW	W	EH	LH	H	FR	UAP	LAP	C	D	U	I	?
P. b. fasolti (53)	29	30	95.3	0.56	30	1			6	3		2	7		4	8		–		5		
P. b. zonatus (5)	25	45	91.3	0.39	29	1			5	4		2	3		3	6		7				8
P. b. zonatus (P1)	11	35	98.8	0.30	26	1		6	2	3		8	4			2	5				7 (ONSEUP)	
P. b. zonatus (6)	20	40	89.9	0.27	18	2			1			4	3		6	7		3		5		8
P. b. zonatus (41)	13	41	93.8	0.21	22	3					2			1			5	7		4	8 (DANGLE)	6
P. b. zonatus (73)	20	38	89.7	0.16	–		6			3				5	1	2	8	4				7
P. b. zonatus (69)	13	40	94.8	0.13	–		2	3	1	6		4	6			5	5	7				8
P. c. triangularis (85)	19	28	93.1	0.46	46	1			5	3		4	2			6		–		7	8 (PRDEGR)	
P. c. cupula (P3)	10	37	98.9	0.32	19	1			7		4			2	2	7	3		3		5 (ALDIVW) 8 (PSANGL)	6
P. c. cupula (41)	35	40	85.8	0.28	18	2			6	1		4	3		3	8	7	6	7	5		
P. c. dalli (4)	15	36	93.2	0.16	–		4	6	7			2	1		3	7	8	5				

4. Standardized widths and heights: 4 axes if early widths and heights sort separately from later widths and heights: EH, PRW (since protoconch width is the dominant influence), EW and LW. 2 axes if all widths and all heights sort together: W and H.

5. Standardized color variables: C.

6. Others:

a) In two cases, the measures of doming, which usually are grouped with early heights, sort with their own axis: D.

b) I ("independent"), single reference axis variables sorting independently of all others. (The "independence" is, of course, only relative since reference axes are not mutually orthogonal in the oblique solution.)

c) ?, Small groups of unclear significance. These are confined to the last three axes and would be dispersed early during a series of successive reductions.

The information of Table 7 supports conclusions derived from the Government Quarry sample in the following ways:

1. Absolute size is the dominant factor in interrelationships of non-standardized variables: As the range of size within a sample decreases, the effect of size upon variable interrelationships declines in the following ways:

a) A smaller percentage of variables sorts with the "size" axis. In *P. cupula cupula* from locality 41, for example, WHORLS (always an important member of the "size" cluster when the range of size is large) associates negatively with later widths. A shell which is large at late whorls will tend to have fewer whorls at its final size.

b) The "size" cluster, which always associates with the first axis when the range of size within a sample is large, groups with progressively lower axes as the size range decreases.

c) When the size range within a sample is small, the widths and heights of size-dependent measures sort separately. This recalls the *Rana pipiens* example cited earlier. Forelimb and hindlimb clusters are lumped together when the level of correlation used to form groups is too low to permit a distinction. Likewise, a wide size range swamps more subtle relationships within the group of measures that it

controls. At small size ranges, the dominant effect of size is diminished and the separation of widths from heights is made, just as forelimb and hindlimb clusters of *Rana pipiens* are disassociated at high levels of correlation.

2. Certain non-standardized variables show a high degree of independence from the set of size controlled measures:

a) Measures of the upper part of the outer apertural lip: In 8-axis solutions these form a distinct cluster in all but one of the analyses. Only in the *P. bermudensis zonatus* from locality 41 do these measures sort with the "size" axis.

b) Ratios related to the form ratio of the shell (WIDIVH, ALDIVW and RELSPI): These tend to group with the "size" axis when the range of size within a sample is large, and with the "form ratio" axis when it is small.

c) UMBILC: Virtually size-independent (in the absolute sense), umbilical width constitutes its own axis or sorts with the form ratio assemblage as a mechanical correlate of relative shell width.

d) CALLUS: Absent in *P. cupula*, its associations are very erratic in *P. bermudensis zonatus*, though it never associates with the "size" axis. In four of six cases, it occurs in a group of uncertain significance; it is negatively related to standardized widths in two other instances.

3. Standardized widths and heights tend to sort in four groups:

a) Early heights and measures of doming intensity group together. KVALUE and INFORM sort with early heights in four of ten cases.

b) Protoconch width controls the width of early whorls. Its influence is not overcome until the shell has grown to a size at which the contribution made to the total width by the protoconch becomes negligible. In these analyses, WIDTH1 is invariably associated with the protoconch. In only two of eleven cases has WIDTH2 overcome the protoconch influence to sort with later widths; WIDTH3 sorts with later widths in five cases. WIDTH4 is associated with protoconch width in only one case, WIDTH5 never.

c) Late heights and widths sort discretely or with measures of the form ratio assemblage.

4. In an 8-axis solution, color variables tend to constitute a discrete group. Of all morphological features, they show their strongest relationship with the wide protoconch and relatively high shell groups. This conclusion is confirmed in a rough way by these additional data. In six cases, a color measure (or measures) is joined with variables of these groups. This relationship cannot be completely general, however, for in another case (*P. cupula cupula* from locality 41) color measures project *negatively* on the protoconch width axis.

In addition, these data provide new information:

1. Measures related to the subperipheral part of the outer apertural lip also tend to sort independently of size in an 8-axis solution, though their independence is neither as frequent nor as strong as that of corresponding measures of the upper part of the outer apertural lip.

2. A test of redundancy is provided by the observation of invariant similar sorting of a pair or group of variables. RELUMS is a function either of its numerator or denominator. WIDTH1 is invariably related to the protoconch width. PSANGL and RATIO5 measure the height/width ratio at the end of the fifth whorl; only the latter need be used. UPPECC and LOWECC are functions of their numerators; the raw measures UPPOFF and LOWOFF may be considered alone. HALFAP is never independent of the height of the aperture. Sokal (1962) has cited the recognition and elimination of redundancy as a major aim of factor analysis: "Thus the investigator may avoid the redundancy of using characters which only duplicate information already obtained and hopefully approach closer to the ideal of the study of variation

of genetic factors rather than of morphological characters" (1962: 228).

VI. THE EVOLUTION OF *POECILOZONITES CUPULA*

A) The Nomenclature of Diversity

1. *The recognition of P. cupula.* *P. nelsoni* and *P. bermudensis* have long been recognized as major assemblages of wide temporal and geographic extent. Heretofore three minor "species" known from one or a very few localities have been included in the subgenus: *P. cupula* Gulick 1904, *P. dalli* Gulick 1904, and *P. cupuloides* Peile 1924. Collections made from every known snail-bearing locality in Bermuda furnished additional specimens of all three and several new samples that would merit specific distinction under criteria previously employed. Yet the minor types, the new samples, and several collections previously classified as small *P. bermudensis* (in Sayles, 1931) share features of color, form, and distribution sufficient in extent to merit their union into a single polytypic species, *P. cupula*. The diversity of basic form among subspecies of *P. cupula* is great, ranging from 18.4 to 25.5 mm in size at the fifth whorl and from 0.68 to 1.61 in width/height at the fifth whorl, but convergences that continually arise in gross measures of size and shape make these features unsuitable by themselves as criteria for specific discrimination.

Pulmonate systematists have relied heavily upon variation in color banding, at first with "intuitive" feeling for a "good" character, later with the confirmation that banding patterns are often controlled by a simple genetic mechanism—a series of multiple alleles or closely linked genes (Ford, 1964). The basic measures of size and form ratio cannot always distinguish *P. cupula* from *P. bermudensis*, for whereas the latter tends to be larger and relatively wider at the fifth whorl, there is overlap between its smallest members and the largest *P. cupula*. Color patterns, however, permit a complete separation: *P. cupula* displays distinctive band patterns not seen in *P. bermudensis*, never develops a supplementary color wash below band 3, possesses sharp band margins, and never exhibits the "faded" variation (see Chapter 8, section A). No single feature of size or shape can make such a distinction: The parietal callus (absent in *P. cupula*) comes closest; it is invariably present in *P. bermudensis zonatus* but is lacking in its derived subspecies. When all measures of size and shape are considered simultaneously by multivariate methods, virtually complete discrimination is provided.

2. *Infraspecific variation.* One of the most lively issues in pulmonate studies concerns the taxonomic recognition accorded to complex patterns of geographic variation within species. Of *Cerion* in the Bahamas, Mayr and Rosen write: "Every colony appears somewhat different from every other one" (1956: 2). The problem is especially acute in *Achatinella* (Welch, 1938, 1942, 1958) and *Partula* (Crampton, 1916, 1925, 1932); each valley is known to harbor its distinctive population of snails. Such exuberant variation within species led Crampton to establish a hierarchy of infraspecific categories to encompass the diversity. This "scale of subspecific divisions of various grades, down to the groups of individual variants which are essentially identical," (Crampton, 1932: 185) included, in descending order, the variety, socius, cohort, and gens, the last defined as "individuals which are exactly alike in at least one distinguishable character" (1932: 186). Welch erected large numbers of subspecies, relying on a largely arbitrary criterion: "If area A contains shells which are distinct from area B so that the color patterns of the shells can readily be separated 90 per cent to 100 per cent, the demes are considered to be distinct subspecies and given a latin name . . . All demes in which the phenotypes of shells are less than 90 per cent distinct are called microgeographic

races" (Welch, 1958: 130). Such criteria led to the distinction of 78 subspecies and 60 additional unnamed races of *Achatinella apexfulva* (Welch, 1942).

And yet to speak of this infraspecific diversity as a "problem" seems absurd, for it is precisely such morphological variety and its geographic distribution that has provided the major source of information for an understanding of evolution at the species level. It becomes a problem and not a source of delight only when the allocation of names in the quest for an ordering of natural diversity is deemed more important than the search for an understanding of the causes of that diversity. And the former preference seems anachronistic not only in groups for which the so-called "alpha taxonomy" is accomplished, but also perhaps for all infraspecific variation.

Other authors have avoided formal recognition of infraspecific units altogether, hoping thereby to render the evolutionary information more readily accessible. Kincaid, commenting on the work of Welch, writes (1964: 6): "It seems unfortunate that the literature should be burdened with such extensive taxonomic terminology to describe what is essentially an interesting biological phenomenon illustrating one phase of organic evolution. It indicates clearly, however, the difficulty under which taxonomic science suffers in dealing with a problem of this type." Kincaid used the informal term "morph" to delimit 53 demes of the polytypic prosobranch species *Thais lamellosa*. Likewise, Johnston and Selander (1964) have refrained from erecting trinomials for North American house sparrow populations: "Current taxonomic practice gives formal nomenclatural recognition, at the subspecific level, to morphologically definable geographic segments of species populations. . . . Although application of subspecific trinomials to certain New World populations of sparrows would be fully warranted, we are not convinced that nomenclatural stasis is desirable for a patently dynamic system" (Johnston and Selander, 1964: 550).

The primary sin of most infraspecific (and much specific) nomenclature in paleontology has been the naming of mere shapes without sufficient concern for whether the distribution of such shapes is consistent with their existence as a biological population. Thus, the finding that a pulmonate subspecies *alba* is invariably associated with colored shells of similar form should suggest polymorphism within a single population and render a subspecific categorization inappropriate. Each discernible infraspecific unit in *P. cupula*, however, has a geographic range in which it alone resides and a non-disjunct distribution in time—i.e., each distinct morphological entity seems to represent "an aggregate of local populations of a species, inhabiting a geographic subdivision of the range of the species, and differing taxonomically from other populations of the species" (Mayr, 1963: 348). After presenting this definition of subspecies, Mayr cautions against dignifying each slightly different local population with a trinomial. The diversity in *P. cupula* is so great that every sample displays some characteristic feature of size, shape, or color. To supply each of these with a name would be to construct a static morass of formalized verbiage unapproachable to all but the most specialized readers; and it is, I fear, the wholesale erection of such imposing subspecific arrays that has rendered some of the finest evolutionary works on pulmonate diversity virtually unreadable. To formalize no infraspecific terminology would, on the other hand, be insufficiently expressive of the vast amount of morphological diversity that often prevails within a pulmonate species. Fortunately, a *via media* is available for *P. cupula*—the distinctive individual samples group into well-defined morphological aggregates, each of which, as mentioned above, occupies a range of space and time consistent with that required of the neontological subspecies. Of the five sub-

species of *P. cupula* named in this work,[1] three are the degraded species of previous authors and two are new. Only one (*P. cupula dalli*) is known from a single locality. Sylvester-Bradley (1956: 67) has written in his contribution to a symposium on paleontological species: "At one time paleontological research tended ever to promote varietal names to specific level, thereby increasing the burden of nomenclature. Now it is the reduction of a specific name to variety or subspecies that is a sign of increasing knowledge." And Thomas (1956: 27), in the same symposium, writes: "The existence of geographical subspecies in neontology behoves their recognition in fossils."

B) The Description of Diversity

1. *Diversity of Color.* The conservatism of color banding in *P. bermudensis*[2] stands in marked contrast to the variety of patterns known in *P. cupula.* The 21 samples of *P. cupula* may be allocated to two complexes on the basis of a primary dichotomy in banding patterns. The basic stock (*P.c. cupuloides. P. c. triangularis, P. c. dalli,* and *P.c. multispira*) here termed the polymorph complex, is characterized by the following fourfold polymorphism:

a) flames present in the position of band 1 at the fifth whorl, no other color: 1^f00 (see Chapter 4 on band numbering system)

b) flames present in the position of band 1 at the fifth whorl, band 2 absent, band 3 present: 1^f03.

c) band 1 absent, band 2 present (usually as a line), band 3 present; three subtypes (see footnote): 02^n3, 023, and 0(23)

d) flames present in the position of band 1 at the fifth whorl, bands 2 and 3 present; band 2 as a line: 1^f2^n3.

The second stock, coextensive with the subspecies *P. cupula cupula*, invariably exhibits a single banding subtype in which all three bands are present, the second as a line: 12^n3. The band pattern of *P. cupula cupula* is most plausibly derived by stabilization of polymorph type d and subsequent intensification of coloration in the band-1 position.

Table 7 summarizes information on color banding for all samples of *P. cupula.* The following information is given: locality, age (refer to Table 1), name of subspecies, color types present in each sample, and number of shells of each type. The distribution of color types within the polymorph complex displays some notable features:

a) The earliest (Walsingham) samples of the polymorph complex exhibit the complete range of shell polymorphism; no younger population displays more than three of the four morphs.

b) The four morphs are ranked in order of increasing intensity of coloration: a (1 flame, no bands), b (1 flame, 1 band), c (2 bands) and d (1 flame, 2 bands). When fewer than 4 morphs are present in the sample, their distribution is always non-disjunct; a and b, b and c, or c and d may occur but never a and c, a and d, or b and d.

2. *Diversity of form.* To provide a picture of the prolific morphological diversity of *P. cupula*, the following account presents the defining features of subspecies and lists the recognizable local populations of each. The basic form of the shell can be encompassed by four measures: the size at the

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[1] Formal taxonomic descriptions will be found in Appendix 1.

[2] Only 023 and 123 and its subtypes are found in *P. bermudensis.* A subtype is defined as a member of a group linked by intermediates within the population. Fused and unfused bands and presence or absence of the supplementary color wash are subtypes in *P. bermudensis*: 123, 1(23), (123), 1(23)S, 123S and 12(3S) (see Plate 5, Figs. 3, 4) are all subtypes of a type. Although direct confirmation is obviously impossible, it is tempting to draw the implication that types are genetically distinct, while variation within subtypes of a type (which vary only in intensity of pigmentation and not in band positions) are either phenotypic expressions of a similar genetic system or under the control of genes whose primary effect is not the regulation of color (e.g., factors controlling the general growth rate).

TABLE 7. GEOGRAPHIC AND TEMPORAL DISTRIBUTION OF COLOR PATTERNS IN *POECILOZONITES CUPULA*. The following information is given for each sample: Loc, the locality number; trivial name of the subspecies; color types present in sample; and N the number of specimens displaying each type.

	Polymorph Complex				*P. cupula cupula*			
Formation	Loc		Color	N	Loc		Color	N
Harrington-	84	*multispira*	c) $02^{n}3$	15	35	*cupula*	$12^{n}3$	157
Pembroke	88		d) $1^{f}2^{n}3$	5	37			
	4	*dalli*	b) $1^{f}03$	8	39			
			c) $02^{n}3$	71	41			
			0(23)	8	43			
			d) $1^{f}2^{n}3$	19	76			
	85	*triangularis*	c) $02^{n}3$	3	77			
			d) $1^{f}2^{n}3$	1	63	*cupula*	$12^{n}3$	11
	46	*triangularis*	c) $02^{n}3$	4				
			023	5				
			0(23)	6				
			d) $1^{f}2^{n}3$	1				
Shore Hills	48	*cupuloides*	c) $02^{n}3$	4	P2	*cupula*	$12^{n}3$	12
			023	1				
			0(23)	8	P3	*cupula*	$12^{n}3$	16
	56	*cupuloides*	a) $1^{f}00$	4				
			b) $1^{f}03$	8				
Belmont	89	*cupuloides*	c) $02^{n}3$	2				
			0(23)	14				
	71	*cupuloides*	c) 023	1				
			0(23)	1				
Walsingham	9	*cupuloides*	a) $1^{f}00$	28				
			b) $1^{f}03$	3				
			c) $02^{n}3$	10				
			0(23)	1				
			d) $1^{f}2^{n}3$	9				
	P4	*cupuloides*	a) $1^{f}00$	22				
			b) $1^{f}03$	6				
			c) $02^{n}3$	8				
			d) $1^{f}2^{n}3$	8				

fifth whorl (S5); the form ratio, width/height, at the fifth whorl (FR5); and the measures of doming intensity (see Chapter 3), the initial form index (InFI) and the differential growth ratio (DGR).[1]

a) *P. cupula cupuloides* (Plate 1, Fig. 3), Walsingham-Shore Hills: Intermediate in all measures of basic form among subspecies of the polymorph complex and geologically oldest, this subspecies may represent the parental stock of all later *P. cupula* subspecies. Several local populations are distinguishable.

i) Quarry Road local population: Shells from Peile's type locality cannot be distinguished from those of the adjacent Quarry Road samples. Both display all four color morphs and almost identical values of the basic form measures (12.1 and 12.0 mm S5, 1.16 and 1.16 FR5, 2.15 and 2.19 DGR, .282 and .278 InFI).

ii) West Coney Island local population: The lighter morphs (a and b) have become stabilized; shells are smaller (S5 = 11.2 mm) and relatively wider (FR5 = 1.30) than those of the Quarry

[1] Cited figures in this discussion are mean sample value of these variables. A complete account of morphological differences among samples is found in the matrix of means, Appendix 3.

Road local population. Differences among local populations are significant at the 5 per cent level unless otherwise noted.

iii) Surf Bay local population: Morph c alone is present (but only 2 specimens have discernible color markings). The set of means for basic form measures of the 7 specimens is distinct but not significantly different, perhaps due to small sample size, from that of other samples.

iv) Bird's Nest local population: Lowest FR5 (1.07) and correspondingly highest DGR and InFI (2.22 and 0.296) for *P.c. cupuloides* populations. S5 (12.0 mm) indistinguishable from Surf Bay and Quarry Road local populations. Morph c alone is present.

v) Ferry Road local population: 13 specimens with discernible color markings are all of morph c. The poorly preserved specimens were not measured.

b) *P. cupula triangularis* (Plate 1, Fig. 5), Harrington-Pembroke: The low doming intensity of this subspecies (only *P. cupula* with mean sample DGR less than 2.00) imparts a more or less triangular cross section to the shell. Since the initial form index is also low, this subspecies is the relatively widest of all *P. cupula*. Morphs c and d are present in both its local populations.

i) Pink Beach Road local population.

ii) Devil's Hole local population: The Devil's Hole population is larger at the fifth whorl (13.2 vs. 12.1 mm); it has a lower DGR (1.85 vs. 1.94), but the correspondingly higher InFI (.247 vs. .220) produces a form ratio insignificantly different from that of the Pink Beach Road population (1.55 vs. 1.61).

c) *P. cupula dalli* (Plate 1, Fig. 2), Harrington-Pembroke: This population of *P. cupula* is unique among all samples of *P.* (*Poecilozonites*): it is the smallest ($S5 = 9.7$ mm), the relatively highest ($FR5 = 0.68$), and possesses the greatest mean sample values of DGR and InFI (2.94 and 0.418). I have previously noted (Gould, 1966a) that all these features are interrelated. Since progressively larger values of the differential growth ratio imply continually more rapid increases in the height/width ratio during ontogeny, a high differential growth ratio will be size-limiting. A *P. cupula dalli* of just twice maximum width would possess a shell six times higher than wide.

i) Albuoy's Point local population.

d) *P. cupula multispira* (Plate 1, Fig. 4), Harrington-Pembroke: At the fifth whorl, *P. cupula multispira* is no larger than *P. cupula dalli*. Yet large individuals of this subspecies reach sizes unexcelled by any other *P. cupula*. All other populations of *P. cupula* (and of *P. bermudensis*, for that matter) show a surprising stability in average whorl numbers of large specimens (always between 5 and 6½). *P. cupula multispira* is unique in exceeding this number; the largest specimen in my collection has 7⁶⁄₈ whorls. Since the largest specimens reach relative heights even greater than that of *P. cupula dalli* at the fifth whorl, A. Haycock (correspondence with E. G. Vanatta in collection of the Philadelphia Academy of Natural Sciences) allocated these specimens to *P. cupula dalli*. Though they overlap in this one feature of form ratio, the two subspecies are as distinct from one another as any two taxa of *P. cupula*, and the misallocation serves to indicate the pitfalls of a single-character taxonomy.

There is an element of mechanical inevitability in the mode of production of certain shapes in accretionary structures. We know that the high spire of large *P. cupula multispira* cannot be attributed to a high differential growth ratio. High differential growth ratios, unless accompanied by a low initial form index or extremely large early whorls (see discussion on doming factors in Chapter 3), are severely size limiting (Gould, 1966a). Since the mean initial form index of *P. cupula multispira* is average for polymorph *P. cupula*, the high dome must be attributed to the third doming factor—extremely small protoconch and early whorls. *P. c. multispira*'s

mean differential growth ratio of 2.24 is average for *P. cupula*, but any differential growth ratio greater than 1 implies continual increase in the height/width ratio. *P. c. multispira* is high spired because an average differential growth ratio began operating at an unusually small size. (The differential growth ratio is measured from the termination of whorl 2 to the end of growth; that *P. c. multispira* has an unusually large number of whorls at the size of an average *P. cupula* adult implies, indeed, that the protoconch and initial whorls are small.) Thus, *P. cupula dalli* and *P. cupula multispira* illustrate two of a strictly limited number of pathways to the attainment of a high spire, and the maximum size attained by each subspecies is a function of the chosen pathway.

i) St. David's Island local population: Three localities (84, 88, and 91), the shells of which cannot be distinguished.

e) *P. cupula cupula* (Plate 1, Fig. 1), Shore Hills-Pembroke: The nominate subspecies of *P. cupula* is distinguished from members of the polymorph complex by its unique banding pattern ($12^{u}3$) and features of morphology discussed below (larger size and different DGR vs. InFI relationship).

i) South Shore local population: Found at five localities (35, 37, 39, 41, 43) along a relatively continuous outcrop of Harrington or Pembroke accretionary zones running for 1700 m along the South Shore from Spencer's Point to Devonshire Bay; also present at two localities (76, 77) on Knapton Hill. Next to largest and relatively widest (a function of lowest DGR and InFI) of the local populations of *P. cupula cupula*, large specimens bear an uncanny similarity to shells of some *P. bermudensis zonatus* samples (the possibility of introgression will be considered in Chapter 10). Sayles (1931) allocated specimens from these localities to *P. bermudensis*.

ii) Gibbet Island local population: Smallest population of *P. c. cupula;* intermediate in other respects.

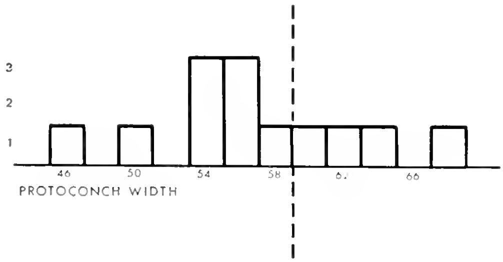

Figure 9. Histogram of mean sample values of protoconch width in *P. cupula* showing complete separation of *P. cupula cupula* from the polymorph complex (left of vertical line). Values on obscissa are midpoints of class intervals (micrometer units at 1 unit = .0327 mm).

iii) Whitby local population: Intermediate in all basic features of morphology, the Whitby population is unique in the narrowness of color band 3. Average relative width for this band is .099, while the range for all other *P. c. cupula* is .166 to .200.

iv) Walsingham local population: These shells from the species' type locality are the largest (S5 = 14.0 mm) and relatively highest (R5 = 0.97) of *P. cupula cupula* samples.

On the basis of color patterns alone, a primary dichotomy was made between *P. cupula cupula* and members of a "polymorph complex" (*P. c. cupuloides*, *P. c. triangularis*, *P. c. dalli*, and *P. c. multispira*). The following differences in size and shape reinforce the validity of this separation.

a) *P. cupula cupula* is larger at the fifth whorl. Of the polymorph complex, only the Devil's Hole local population of *P. c. triangularis* exceeds the smallest *P. cupula cupula* population (Gibbet Island) in S5. There is no overlap in protoconch width; that of the smallest *P. c. cupula* exceeds that of the largest polymorph population (Fig. 9). If we assume that *P. cupula cupula* was derived from *P. c. cupuloides* by stabilization of morph d and intensification of coloration in the band-1 position, then the correlation of morph type and size at the fifth whorl in the Quarry Road

TABLE 8. CORRELATION OF SIZE AND COLOR MORPH TYPE IN THE QUARRY ROAD LOCAL POPULATION OF *P. CUPULA CUPULOIDES*

Morph	a	b	c	d
Mean size at fifth whorl	11.86	12.23	12.13	12.48
Number of specimens	12	3	6	5

local population of *P. c. cupuloides*, shown in Table 8, assumes special importance. The mean S5 for shells of morph d is larger than that for shells of morph a, and the difference is significant at the 5 per cent level ($0.02<p<0.05$; $t=2.29$ at 15 d.f.). That this correlation of size and morph type holds not only within but also among samples is illustrated by the West Coney Island population, which has stabilized morphs a and b and is the smallest *P. c. cupuloides* (S5 = 11.2 mm). The two measured populations of *P. c. cupuloides* which have stabilized morph c are intermediate in S5 (12.0 and 11.9 mm) between the Coney Island snails and morph d shells of the Quarry Road population. Thus, size and morph type are correlated among shells of a population, among populations of a subspecies, and between subspecies of an inferred ancestor-descendant sequence in *P. cupula*. Although the genetic cause of the correlation is probably unknowable,

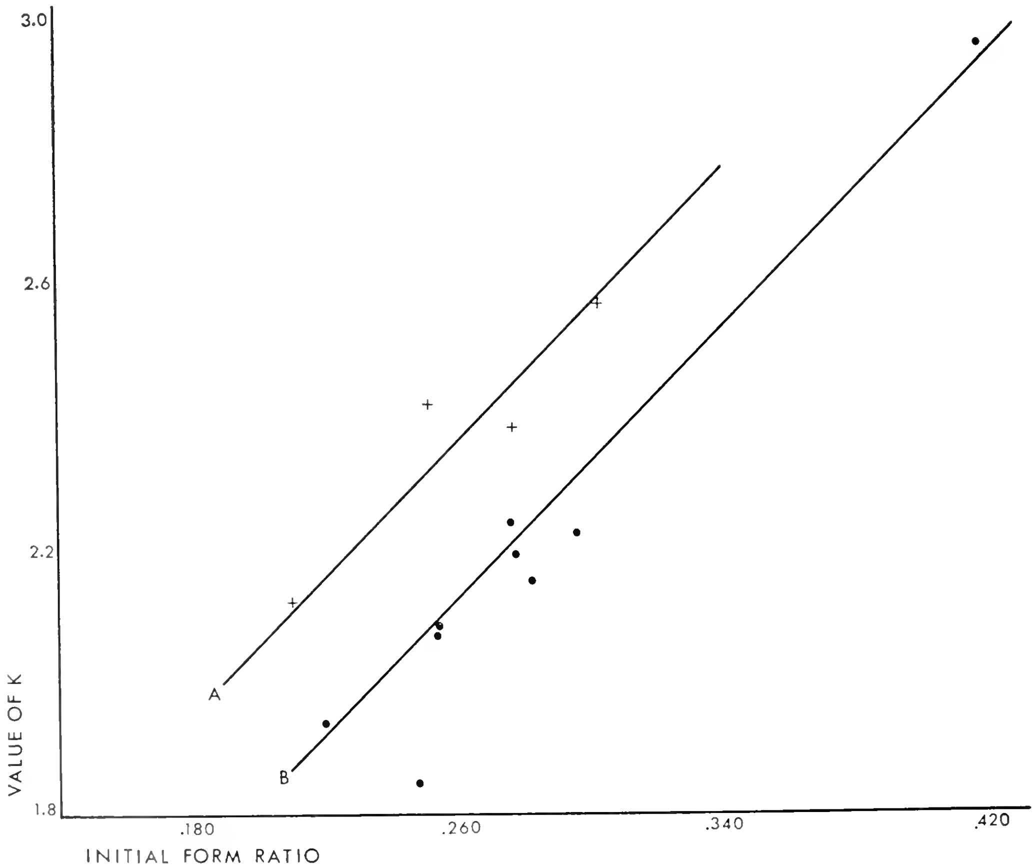

Figure 10. Differential growth ratio vs. initial form index for all *P. cupula* samples. Polymorph complex samples on lower regression, *P. cupula cupula* on upper (with South Shore local population samples grouped as a single grand sample).

this example does demonstrate that color variation may have morphological correlates and that the adaptive significance of a color pattern need not reside exclusively in the pattern itself.

b) Figure 10 shows the relationship between DGR and InFI for mean sample values of all measured *P. cupula* samples. The data are well approximated by two parallel lines for *P. cupula cupula* and the polymorph complex, respectively. At equal values of the differential growth ratio, *P. cupula cupula* tends to have a lower initial form index and, correspondingly, a relatively wider shell than members of the polymorph complex of the same size.

In addition to providing a discriminatory index, this relationship illustrates a point often overlooked in correlation studies. Among individuals of a population, the correlation of InFI and DGR is *always negative* (reaching values as high as -.727 for the *P. c. cupula* South Shore local population, and -.789 for *P. bermudensis zonatus* from Government Quarry). Among populations of *P. cupula*, the correlation is *strongly positive* ($r = +.787$ for all *P. cupula* considered together and +.971 for populations of the polymorph complex). This discrepancy ceases to be surprising when we realize that the correlation of InFI and DGR is controlled by different factors within and among populations. A negative correlation implies that later growth operates in the opposite sense to previous development. Stabilizing selection within a population will allow a limited range of adult form ratios. If initial growth in relative height is abnormally rapid (high InFI), the DGR will tend to be low in order to produce a final form ratio within the favored range. Unusually low values of InFI will require a correspondingly high DGR. (I infer from its high variability that the DGR is strongly subject to the influence of feedback from early development.) A positive correlation, on the other hand, implies that early and later growth vary together to produce the final shape. If it is selectively advantageous for shells of one population to be relatively higher than those of another, an increase in *both* DGR and InFI will most efficiently produce the higher spire. Among populations differing in mean adult form ratio, a positive correlation is to be expected.

Given these consistent differences in color and morphology, a case could be made for specific distinction of *P. cupula cupula* from the polymorph complex. Yet such a discussion seems vacuous while morphology alone supplies the evidence, and the more conservative view is adopted here.

A multivariate assessment of morphological differences among subspecies is provided by Q-mode factor analytic plots on varimax axes (Chapter 5, section A). The matrix of means, with mean sample values for non-standardized variables given at $5^{3}/_{8}$ whorls,[1] was used in the analysis. COVAP does not handle missing data, and all the color measures save relative width of band 3 were omitted, since fewer than five measured specimens provided data for the other color variables in many samples. This elimination has the salutary effect of permitting a comparison of size and shape alone (relative width of band 3 is not a strongly discriminating measure).

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[1] Matrices of means for *P. cupula* and *P. bermudensis*, the epitome of all data used in this work, will be found in Appendix 3.

A whorl number (rather than a size) is used for standardization since the whorl number at maximum size varies very little in *P. cupula*; thus, whorl number approaches the ideal of standardization at a developmental stage. This introduces a serious bias only for *P. c. multispira*, the maximum whorl number of which exceeds all other samples by 2. Many of its values confirm the impression that it is being considered at an earlier developmental stage than are the other samples. Its value of "the lower eccentricity," for example, is the lowest of all samples, but since "the lower eccentricity" is the one non-standardized measure which undergoes its greatest change late in ontogeny, this may indicate only that, at $5^{3}/_{8}$ whorls, the *P. c. multispira* sample is developmentally younger than all other samples.

A percent-range transformation was used to eliminate unequal weighting of variables due to differences in their magnitude. (Manson and Imbrie, 1964). Samples are represented on plots by the following numbers:

P. cupula cupuloides
- i) Quarry Road local population: 13, 14
- ii) West Coney Island local population: 15
- iii) Surf Bay local population: 19
- iv) Bird's Nest local population: 18

P. cupula triangularis
- i) Pink Beach local population: 11
- ii) Devil's Hole local population: 12

P. cupula dalli
- i) Albuoy's Point local population: 17

P. cupula multispira
- i) St. David's Island local population: 16

P. cupula cupula
- i) South shore local population: 01, 02, 03, 04, 05, 06, 07
- ii) Gibbet Island local population: 08
- iii) Whitby local population: 09
- iv) Walsingham local population: 10

Figure 11, a plot of axis 1 vs. axis 2 of a 3-axis solution, gives a picture of relative morphological similarity among subspecies as recorded by 32 variables.

a) *P. c. dalli* and *P. c. multispira* are very distinct from all other samples and from each other. Their mutual separation confirms their subspecific status and demonstrates that the similar form ratio of large specimens is a superficial convergence.

b) The local populations represented by more than one sample (Quarry Road *P. c. cupuloides* and South Shore *P. c. cupula*) group as tight clusters in all plots.

c) In the absence of distinctive color variables, the 3-axis plot does not distinguish the samples of *P. c. triangularis* from the South Shore local population of *P. c. cupula* (these are, collectively, the relatively widest samples of *P. cupula*). If a fourth axis is added (Fig. 12), a distinction of the two subspecies is established. Highest projections upon the fourth axis are exhibited by the Whitby and Walsingham local populations of *P. c. cupula*. The South Shore local population projects fairly strongly on this axis, the samples of *P. c. triangularis* very weakly.

d) The three *P. c. cupula* local populations of low fifth whorl form ratio are not well distinguished from the *P. c. cupuloides* cluster in the absence of distinctive color variates. Some weak separation is indicated by the higher joint projections of the *P. c. cupula* samples upon both axes 1 and 2.

Table 9 presents an oblique projection matrix for the 3-axis solution. Again, *P. c. dalli* and *P. c. multispira* are seen to be very different from all other populations and from each other. *P. c. triangularis* is not separated from the South Shore *P. c. cupula*, but the weak distinction of relatively high *P. c. cupula* populations from samples of *P. c. cupuloides* is confirmed by samples of *P. c. cupuloides* is confirmed by the projections of all *P. c. cupula* local populations (higher than that of any *P. c. cupuloides*) upon the sample of the South Shore local population of *P. c. cupula* that serves as the first oblique reference axis.

3. *Distribution of P. cupula in time.* Although temporal and geographic ranges of subspecies can be documented, the arrangement of these populations in a phylogenetic pattern requires some very speculative inference. (The phylogeny of *P. bermudensis*, which, due to far greater sample numbers, sizes and temporal control, can be documented with high accuracy, will be discussed later. The tenuous nature of conclusions concerning *P. cupula* should not be read as a model for the general degree of resolution attainable in these studies.) If the observed ranges represent true ranges, then the following conclusions are probable:

a) *P. c. cupula* arose during Shore

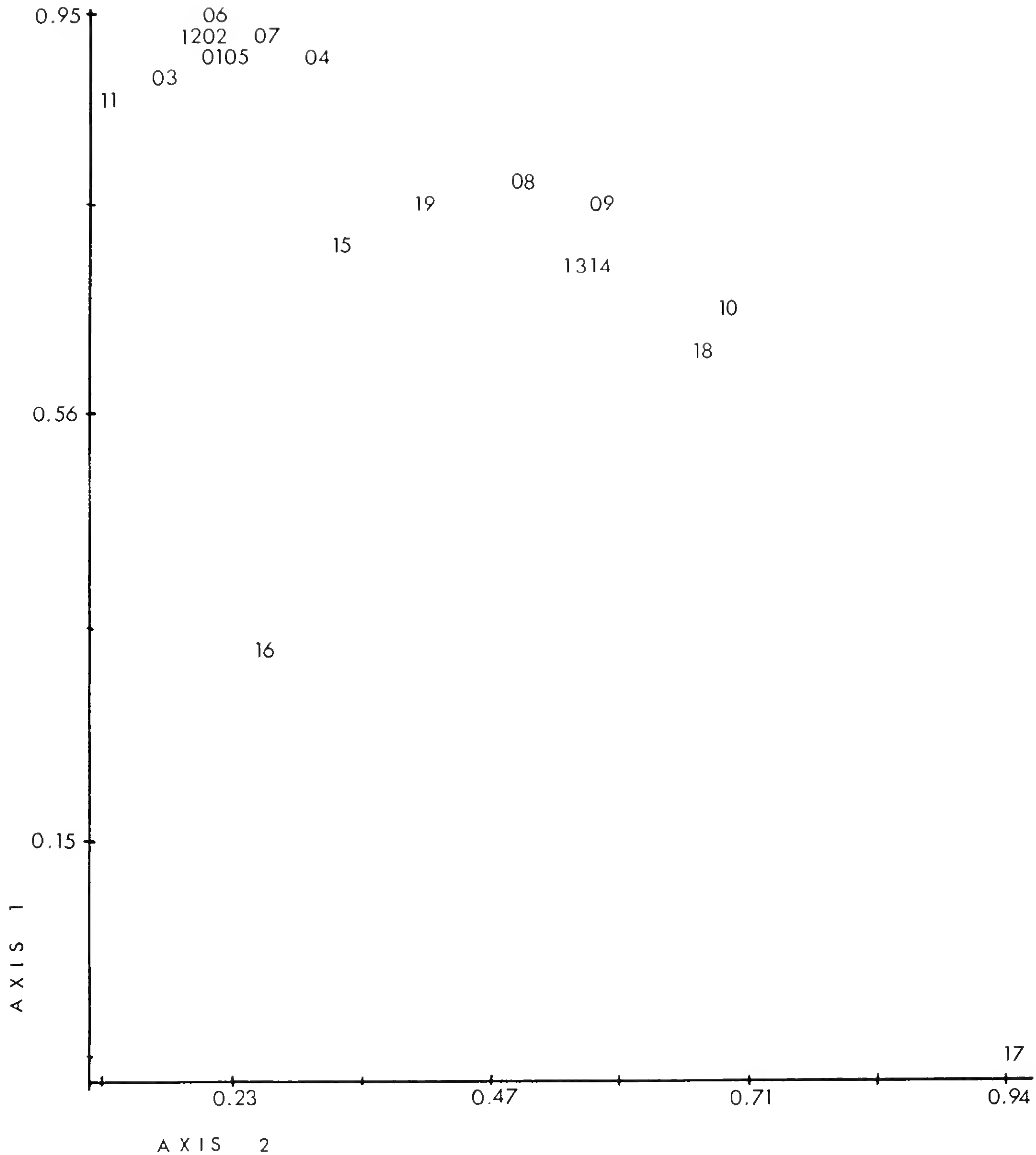

Figure 11. Plot on varimax axes of all *P. cupula* samples.

Hills times from a population (or populations) of *P. c. cupuloides* which had stabilized morph d.

b) The polymorph complex underwent an adaptive radiation, just before the base of the Harrington, which resulted in the extinction of parental *P. c. cupuloides* and the origin of (at least) three new subspecies.

c) All subspecies of *P. cupula* (at least four) became extinct at the top of the Pembroke. Although the first two statements are quite speculative, this third conclusion is well documented. Not a trace

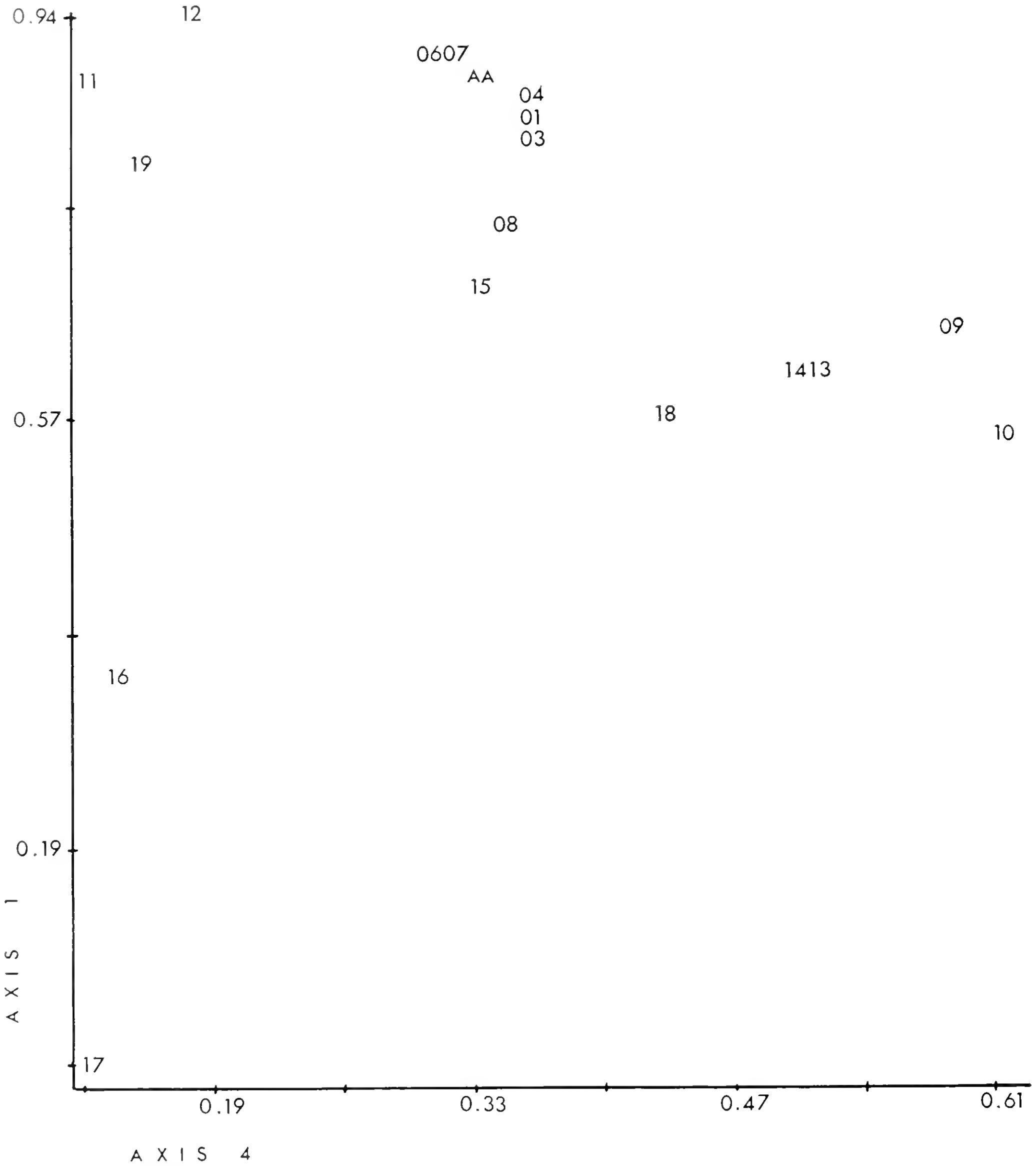

Figure 12. Plot on varimax axes of all *P. cupula cupula* samples. AA stands for 02 and 05.

of *P. cupula* has ever been found in the extensive St. George's and Southampton fossil-bearing formations.

When the subspecies ranges are compared with a chart of inferred sea-level fluctuations (Fig. 13), a basis for interpretation of the phylogeny proposed above is established. The pre-Harrington adaptive radiation is coincident with the rise of the Devonshire sea to a maximum of +5 meters. At such a level, Bermuda would be dissected into even more islands than exist today. A large number of geographically isolated potential habitats

TABLE 9. OBLIQUE PROJECTION MATRIX FOR ALL *P. CUPULA* SAMPLES. The following identifying information is given for each sample: trivial name of the subspecies, name of the local population and locality number when more than one sample of a local population was measured.

Sample	Axis 1	Axis 2	Axis 3
cupula (South Shore, 43)	1.000	0.000	0.000
cupula (South Shore, 41a)	0.987	–0.056	0.050
triangularis (Devil's Hole)	0.967	–0.078	0.057
cupula (South Shore, 41c)	0.950	0.038	0.070
cupula (South Shore, 37)	0.950	–0.080	0.123
cupula (South Shore, 41b)	0.930	–0.051	0.143
cupula (South Shore, 35)	0.895	–0.066	0.194
cupula (Whitby)	0.853	0.380	–0.048
cupula (Gibbet Island)	0.849	0.275	0.039
cupula (South Shore, 39)	0.839	–0.131	0.284
triangularis (Pink Beach Road)	0.813	–0.204	0.320
cupula (Walsingham)	0.792	0.565	–0.141
cupuloides (Surf Bay)	0.767	0.169	0.194
cupuloides (Quarry Road, 9)	0.710	0.332	0.202
cupuloides (Quarry Road, P4)	0.695	0.337	0.216
cupuloides (Bird's Nest)	0.662	0.498	0.104
cupuloides (Coney Island)	0.599	0.031	0.506
dalli (Albuoy's Point)	0.000	1.000	0.000
multispira (St. David's Is.)	0.000	0.000	1.000

would then be available. Rensch (1937) invoked a similar explanation for the diversity of the *Murella muralis* stock in western Sicily. "In the late Tertiary and during part of the Pleistocene, the mountains of Western Sicily were inundated to form islands and peninsulas. Individual mountains were then more strongly isolated than they are today and the stabilization of races was promoted" (translated from Rensch, 1937: 587). The total extinction of *P. cupula* is concurrent with the highest post-Belmont Sea—the Spencer's Point, which rose to +20 meters and virtually inundated the entire island complex. In earlier formations *P. cupula* is often associated with *P. nelsoni; P. bermudensis* rarely occurs with either of the other species of its subgenus. *P. nelsoni* was similarly affected by the Spencer's Point rise, for it is present in the St. George's in only two adjacent localities and is never found in the Southampton. *P. bermudensis*, on the other hand, is quite common in the St. George's and seems to have survived the Spencer's Point inundation with little difficulty. This implies that *P. bermudensis* can adapt itself to dune conditions more readily than other members of its subgenus. Dunes form at the island periphery and, with the drastic reduction of subaerial Bermuda during Spencer's Point time, the remaining land must have been "all periphery," completely effacing the calmer habitats that *P. cupula* and *P. nelsoni* may have preferred.

C) The Cause of Diversity

Adjacent local populations of a pulmonate species are often strikingly diverse, even when a uniform environment seems to prevail throughout the inhabited area. The difficulty of attributing such extreme variability to the effects of natural selection alone has prompted many authors to suggest that random processes of evolutionary change—genetic drift and the founder principle—are acting to initiate, and perhaps even to maintain, the diversity. Mayr and Rosen (1956), commenting on the "crazy quilt distribution pattern" of *Cerion* in Bimini, write: "It is possible and probable that many if not most colonies are founded by a single fertilized adult . . . Each new colony is an evolutionary experiment." At its outset, the new population exhibits gene frequencies different from those of its parental source because the small number of founders cannot be expected to transmit a complete replica of the parental gene pool, but there are also reasons why selection will then promote rapid divergence in a founder population: high inbreeding in early generations, for example, exposes homozygous genotypes to selection more often than in outbred populations (Mayr and Rosen, 1956). Thus, the ultimate genetic separation of the newly-founded and parental populations results both from random genetic attributes of the founders and from

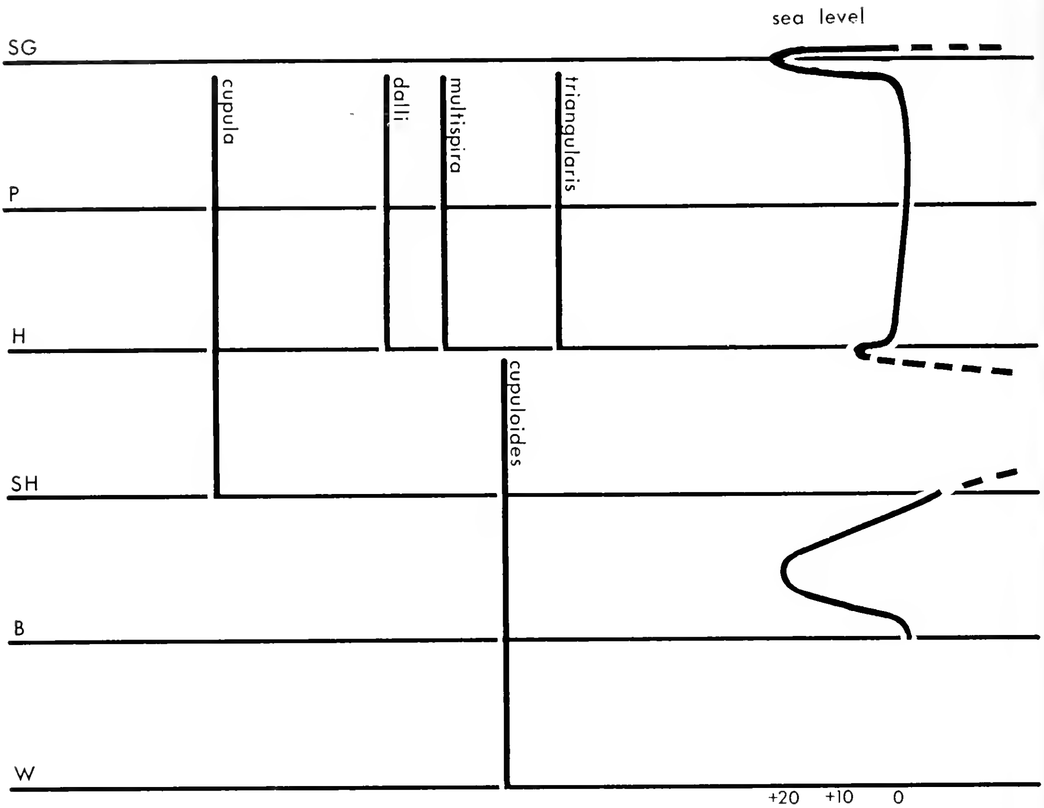

Figure 13. Ranges of the subspecies of *P. cupula*. See text for inferred phylogeny and correlation with rise and fall of Pleistocene sea.

subsequent selection. Komai and Emura (1955) cite the founder principle as "the most important cause of the differentiation of natural populations of this snail [*Bradybaena similaris*]. Besides, there must have been genetic drift due to the small size of breeding population" (1955: 415).

Other authors have responded with a vigorous defense of the total efficacy of selection and some spirited controversies, constituting much of the best recent work on pulmonate microevolution, have ensued. To illustrate the controversy, I have selected the drosophilas of pulmonate microevolutionary studies: *Cepaea* and *Partula*.

a) *Cepaea:* The literature is reviewed by Ford (1964) and Harvey (1964) and will not be extensively cited here. Morph frequencies within populations are known to be strongly influenced by visual thrush predation (cryptic coloration is afforded by different morphs in different environments or during seasonal fluctuations of a single environment), and by varying environmental tolerances of the morphs. Lamotte (1951) maintained that dissimilarities among colonies were due more to genetic drift than to selection, but his reasons have been disputed by later authors. He found, for example, that differences among smaller colonies are greater than among large ones, but Mayr (1963) asserts that more precise adaptation is attainable in the uniform habitats of small colonies. Lamotte found no correlation

between morph frequencies of *C. nemoralis* and *C. hortensis* living together on the same background, but Clarke (1960) showed that similar cryptic patterns can be attained by different routes. In uniform beachwoods, where brown coloration is most advantageous, brown unbanded *C. nemoralis* occur with high frequency, but *C. hortensis* shells tend to be yellow with fused bands. "The visible effect, an overall brown appearance, is very similar in both species, but the means of attaining it are different" (Clarke, 1960: 441). Clarke believes that genes for brown ground color may be less advantageous against the genetic background of *C. hortensis* than they are against that of *C. nemoralis*.

The controversy has been reasserted with regard to Cain and Currey's (1963) "area effects"—remarkably rapid shifts in morph frequencies over very small distances. These they attribute to the selective action of cryptic environmental differences, but Goodhart (1963) has emphasized chance genetic assortment in small founding stocks (see also Goodhart 1962). Recently, Clarke (1966) has proposed a selection model for the production of sharp local changes in clines which appeals neither to cryptic (i.e., unobserved) environmental discontinuities nor to the founder principle.

b) *Partula:* Crampton (1932) found no correlation between form and environment for the Partulae of Moorea and assumed that selection had little to do with establishing and maintaining the diversity among local populations. By comparing Mahalanobis distance functions constructed from Crampton's four variables (height, width, aperture height, aperture width), Bailey (1956) found that an invading subvariety is always more dissimilar to the displaced or preinhabiting subvariety than is its related non-invading subvariety; he thus concluded that selection is operating to increase the distinction of sympatric subvarieties: "The invading variety would be visualized as hybridizing with the preinhabiting variety to a limited extent. This would enable natural selection to build up mechanisms to limit further production of these (assumed) less adaptive hybrids" (Bailey, 1956: 365). There are several weaknesses in Bailey's arguments:

i) Bailey shows that selection tends to *preserve* varieties when they invade territory inhabited by others. The *origin* of races may still be attributed to the founder principle.

ii) Bailey maintains that population sizes are too large for genetic drift. This is certainly true now, but we have no idea of the size of the founding populations, the first invaders of a new valley.

iii) Crampton's traits "have not been shown to be neutral or lacking in selection pressure" (Bailey, 1956: 365). This is a straw man often constructed in such arguments: that every trait separating two groups is of adaptive significance does not necessarily imply that the difference arose by selection. Differences established by drift may be less adaptive, but if the founding population is completely isolated, the slightly more advantageous constitution of its parental population is virtually irrelevant.

Although I am myself predisposed to favor explanations giving a dominant role to selection, I find a logical flaw in the arguments of those who would cite selection as a more or less completely sufficient cause. Advocates of random effects construct their argument in this conditional form: "If the results cannot be explained by selection, then random effects must be invoked." Supporters of selection have tried to show that results can be explained by selection,[1] but this denial of the antecedent cannot falsify the statement, for the citation of a possible cause does not confirm its actual operation. I do not consider selective explanations so inherently preferable that their mere consistency with results is

[1] For example, Cain and Currey (1963: 471): "The interaction of selective forces is complex, and seems to leave little scope for purely random effects."

sufficient to deny alternatives. Actual observations of the work of selection (visual predation studies in *Cepaea*) are more confirmatory, but these usually demonstrate the role of selection in maintaining differences among established populations; random effects may be involved in the origin of these differences.

What causes the differences in morph frequencies among local populations of subspecies in the polymorph complex of *P. cupula*? Visual predation by vertebrates seems unlikely. No native Bermudian tetrapod has been observed to eat snails, and no evidence of bird predation has ever been obtained. Smaller enemies may have been important factors in *P. cupula* mortality. Isopods, nematodes, beetle larvae, mites, land planarians, and infusorians are substantial natural pests of *Bradybaena similaris* (Komai and Emura, 1955). Physiological correlates of color conferring resistance to these enemies may have favored certain morphs. Ewers and Rose (1965) found that banded individuals of the Australian marine snail *Velacumantus australis* were less likely to harbor trematode parasites than unbanded specimens. Physiological correlates of color also confer varying resistances to physical factors of the environment. In *Cepaea*, the yellow bandless form is more resistant to high temperatures than pink and banded individuals. Guerrucci-Henrion (1966: 409) believes that most differences in morph-frequencies among populations of *Cepaea nemoralis* are tied to adaptive physiological features linked with the determinants of color. The morphs of *Bradybaena similaris* differ significantly in growth rate and in susceptibility to low temperatures (Komai and Emura, 1955).

One aspect of the temporal distribution of polymorph populations could be interpreted as favoring explanations involving random processes: the oldest populations exhibit all four morphs; geologically younger populations invariably lose at least one and as many as three color forms. A few founding individuals would not be expected to possess the genetic factors for all color forms. Moreover, since the genitalia of *Poecilozonites* suggest the possibility of self-fertilization (see Chapter 2), it is likely that many new populations begin with the genetic information of only a single individual. *Limicolaria martensiana* exhibits four genetically determined color morphs, but various forms are absent in some populations usually the rarest form in the smallest populations (Owen, 1965).

Another observation, however, is more easily explained by selection. Size at the fifth whorl is correlated with intensity of coloration as represented by the morphs; other graded physiological responses may likewise be linked with color. If random processes were responsible for the stabilization of certain morphs, the distribution of these morphs in populations possessing fewer than the complete set would not be expected to follow a definite pattern. Instead, populations with 2 or 3 morphs always possess a graded series (ab, bcd, or cd, never ac, acd, etc.). This would be expected if the stabilization of morphs is a by-product of selection for large or small size at the fifth whorl.

I am therefore caught in the paradox cited above. Observed temporal patterns are consistent with an explanation involving selection alone, but this does not disprove the possible role of random factors. I would be surprised if reduction of color variability in the few chance founders of new populations played no role in the stabilization of morph subsets in post-Walsingham populations of *P. cupula*.

VII. EVOLUTION OF THE *P. NELSONI* STOCK

A) Introduction

1. *Basic features of P. nelsoni.* The size of organisms, as Huxley has remarked, has a fascination of its own. As the sequoia of Bermudian snails, *P. nelsoni* has long at-

tracted special attention from naturalists. Lieut. Nelson, for whom the species was later named, spoke in glowing terms of "a large and delicate *Helix*" so common in Bermuda's caves that in a single instance, "upwards of thirty bushels were recovered without any earth among them" (Nelson, 1840, quoted in Verrill, 1905: 160). Pilsbry, too, noted its "remarkably large" size (1888: 290).

The type specimen of *P. cupula multispira*, largest known individual of its species, measures 34.2 mm in height plus width, while a *P. bermudensis zonatus* from Charles Island reaches a size of 42.1 mm. In contrast, the largest *P. nelsoni* (Shore Hills Soil, Main Fissure, Government Quarry) measures 77.6 mm and specimens exceeding 70 mm are common in many localities.

The other distinguishing features of *P. nelsoni* are all related to its size. In most samples, mean size of the protoconch exceeds that of other taxa. Since the protoconch fills the egg and since larger snails tend to lay larger eggs (Rensch, 1932), this observation should entail no surprise. The larger protoconch implies larger size at subsequent whorls but this differential is not sufficient to account for the size of *P. nelsoni*. At the fifth whorl, the largest *P. nelsoni* exceeds the largest five whorled *P. bermudensis* by only 8 per cent. Most of the difference in size is related to the greater whorl number of *P. nelsoni*. An 8-whorled specimen is not uncommon, while *P. cupula* and *P. bermudensis* (with the exception of *P. cupula multispira*) rarely exceed six whorls. The mean differential growth ratio of *P. nelsoni* is less than 2.0 in 15 of 21 samples; in *P. cupula* and *P. bermudensis* such low values are characteristic only of *P. cupula triangularis* and some paedomorphic samples of *P. bermudensis*. The higher the differential growth ratio, the faster the increase of height vs. width in ontogeny. If not counteracted by low initial form index or unusually large early whorls, high differential growth ratios limit final size by rapid production of a disadvantageously high spire (Gould, 1966a). The moderately large early whorls and low differential growth ratios of *P. nelsoni* allow this species to maintain reasonable proportions to sizes at which *P. cupula* and *P. bermudensis* would possess a spire too high for efficient locomotion (Gould, 1966a: 1135).

2. *The biospecies in paleontology.* To many paleontologists, the infusion of population thinking has meant only that the normal curve should replace the holotype as a reference standard for the definition of species. The winnowing of a few biologically meaningful taxa from masses of names erected for individual variants has been the most satisfying result of this replacement. Indeed, in most paleontological studies, application of the biological species concept cannot progress much beyond this morphological criterion of species recognition. And yet, the biospecies is primarily an ecologic notion in that the criteria used for inferring the genetic relationships that lie at its core are not those of morphology, but rather those of habitat, behavior, and geographic distribution.

Faced with the dilemma that nonmorphological information is rarely provided by fossils, must the paleontologist abandon the biospecies as inapplicable to his studies (as Weller, 1961, has proposed)? My qualified "no" is based on two arguments:

1. A general statement: Unless a theoretical concept is thoroughly non-operational, in which case it may be reasonably abandoned as meaningless, practical difficulties in application do not demand rejection.

2. A strategy: While admitting that most fossil occurrences do not provide the nonmorphological information needed to define a biospecies properly, I would argue that a paleontologist particularly interested in the study of species ought to seek those

favorable cases in which such information is available.

The Bermudian Pleistocene is a favorable case. Within a span of time far shorter than the margin of error in most geologic correlations, 10 island-wide stratigraphic units have been established. Some, the Harrington unindurated zone in particular, are of such limited temporal extent that geographic distributions for a given instant may reasonably be inferred from the fossils found within them.

Given this degree of resolution, the non-morphological information crucial to many taxonomic decisions becomes available. In particular, we now have criteria for determining whether two samples sufficiently distinct for taxonomic separation are subspecies or species. This is a decision that simply cannot be made without non-morphological information. The standard paleontological use of subspecies to express morphological differences smaller than those required of species, does not automatically provide taxa in accord with the biological definition of this rank;[1] for we know that one of a pair of species is often more similar to the other in size and shape than it is to the subspecies of its own polytypic taxon. Since species and subspecies are defined by interbreeding relationships that can often be inferred from geographic distribution, we have the following criteria to supplement our morphological base:

1. Non-interbreeding sympatric populations are species. (In fossils: biomodality not due to sexual dimorphism, age, etc., among specimens from a single locality not coagulated by *post mortem* transport.)

2. Potentially interbreeding allopatric local populations are subspecies. (A group of fossil samples, each of distinct morphology and each occupying a discrete, non-overlapping portion of the species' total geographic range at a given moment in time.)

[1] I am not suggesting that this practice be abandoned, but merely pointing out that it represents a use of the Linnaean system more for the cataloguing of morphological diversity than for the understanding of biological relationships.

B) History of the *P. nelsoni* Stock

1. *Previous work and new recommendations.* The existing subspecific classification of *P. nelsoni* is a compendium of shapes established by typological systematists before the geology of Bermuda had been unravelled. Five names are available:

1. *P. nelsoni nelsoni* (Bland) 1875. "Normal" samples having a weakly developed callus and adult width/height ratio of about 1.5 to 1.7 have been referred to the nominate subspecies. (Pl. 2, fig. 3).

2. *P. nelsoni discoides* Gulick, 1904. Gulick (1904: 416) suggested the name *discoides* "merely as a convenient term" for low-spired but otherwise "normal" specimens. Verrill (1905) and all subsequent authors have treated this suggestion as a formal trinomial (Pl. 2, fig. 1 is the holotype).

3. *P. nelsoni conoides* Verrill, 1905. Although he acknowledged that "this variety passes into the others by all intermediate gradations," Verrill (1905: 163) gave formal recognition to "the high-spired or conical form of this species, in which the height is from two-thirds to nine-tenths the diameter of the shell, or sometimes equal to it" (Pl. 2, fig. 4 is a topotype). Verrill (1905) describes the type locality of this form as "Western shore of Castle Harbor in a mass of red-clay and stalagmite." Haycock's label (collection at the Bermuda Museum) for his *P. n. conoides* specimens lists their source as "Gulick's locality 806, the types for Verrill's *P. conoides*." Now Gulick's 806 is also the type locality of *P. n. discoides* and, indeed, Gulick listed the extreme shapes for shells of this locality as Alt. 34, Diam. 34 mm (a typical *P. n. conoides*) and Alt. 19.5, Diam. 39 mm (the type specimen of *P. n. discoides*); Gulick designated only the low-spired individuals as *P. n. discoides*. This locality has been

obliterated by progress and now underlies a sand trap of the Castle Harbour Hotel golf course.

The snails assigned to this subspecies were found in fissures of a Walsingham cave filled with Shore Hills Soil. We do not know whether the two names represent the artificial division of a single variable sample or the fossil remains of two different fissures. Despite the tremendous diversity of form among samples, I have never made a collection in which the range of within-sample variability was even nearly sufficient to encompass these two extremes in spire height. On the other hand, the caves and quarries of this area are studded with soil-filled fissures. The fissures were filled at different times within the Shore Hills, and each of several fissures within a locality may contain a distinctive fossil sample. I suspect, therefore, that the names *P. n. conoides* and *P. n. discoides* were applied to morphologically coherent samples from different fissures of a single locality.

4. "*P. nelsoni gulickiana*." Though it never appeared in print, Pilsbry intended to establish this taxon for a sample from Locality P3, for he wrote the following Latin note: "n. subsp.: P. n. callosus Gulicki prop., sed major carina validior et color diff. P. nelsoni gulickiana Pils." [Close to Gulick's *P. n. callosus*, but stronger carina . . .] The color pattern of these shells, 1f23, is the usual one for *P. n. nelsoni* (to which this sample is most closely related despite Pilsbry's statement); *P. n. callosus* (discussed below) is 023. (Pl. 2, fig. 6 is the specimen which would have been made the type of this taxon.)

5. *P. nelsoni callosus* Gulick, 1904. The holotype (Pl. 3, fig. 2), from "Benj. Trott's sand pit, Tuckerstown," represents a group of samples distinguished from other forms of the species by their smaller size, large number of whorls, and prominent parietal callus.

The use of a classification rooted in outdated principles chains us to those principles. My goal in reassessing the classification of *P. nelsoni* is not to establish a "better" order (if such an adjective is even appropriate to human contrivances), but to arrange taxa in accord with modern principles, thereby providing a vocabulary that allows these principles to be discussed. In seeking taxa which correspond to biological populations, two aspects of previous methodologies seem especially obstructive. First the subjective appraisal of morphology based on one or just a few characters should be replaced by a more objective evaluation of many variables and their interrelations. Especially suspect is the subspecific sequence *discoides-nelsoni-conoides*, based as it is solely on the variable character of spire height. Measurement of many characters with subsequent simplification and representation by factor analysis was successful for *P. cupula* and will be used here. Secondly, the naming of mere shapes must be extended to a study of the geographic and temporal distribution of such shapes.

When the second recommendation is followed, some regularities are noted immediately. In particular, the two major lithologies, red soils and eolianites, contain distinct aspects of the total fauna: *P. nelsoni callosus* is confined to eolianites (a persuasive argument for its validity), the other four named taxa to red soils.

2. *Distribution and variation of the P. nelsoni stock in red soils.* Sayles (1931) and Bretz (1960) took as their main paleontological guide to Bermudian stratigraphy the supposed absence of *P. nelsoni* above the Harrington soil. This species is, however, reasonably common in Pembroke dunes and has now been found (by L. S. Land and myself) in the St. George's at adjacent localities 18 and 68; its range, as known today is Shore Hills to St. George's.

The outstanding feature of *P. nelsoni* is its diversity. From sample to sample, differences in basic shape and shell thickness occur in combination with a great variety

of themes on the color pattern 123.[1] Yet variability within samples is not nearly so great (color characters are particularly diagnostic). As in *P. cupula*, almost every sample of *P. nelsoni* is sufficiently unique to allow the unambiguous assignment of a single well-preserved shell to its proper sample. So marked is this distinction that each of several Shore Hills fissure fills of some Bermudian quarries may contain its particular assemblage. Gulick (1904) was sufficiently modern in approach to avoid mixing snails of the same species from different localities, but he lumped fissures within localities, thereby obscuring important patterns of infraspecific variation. In Government Quarry (locality 5), for example, three of the numerous fissures contain large numbers of *P. nelsoni* (while a fourth, dubbed "the graveyard" by local quarrymen, is a massive coquina of *P. bermudensis zonatus*). The "Main Fissure" on the south wall contains large, rather thick shelled, narrowly umbilicate specimens with strong 123 coloration and an angulate aperture with sharp carina. Snails of the "Bird Fissure" (type locality of the crane *Bacopteryx latipes*) are large, thin shelled, and widely umbilicate, with strong 123 coloration and a rounded aperture (Pl. 2, fig. 7). The "Coquina Fissure" on the west wall is filled with small, low-spired, and delicate *P. nelsoni* whose weak coloration is evident in the narrowness of bands 2 and 3 and the persistence of flames in the band 1 position.

Morphological relationships among 24 samples (each represented by the standardized means of 24 variables)[2] are shown in Figure 14, a plot on varimax axes 1 and 2 of a three axis Q-mode solution; the three axes account for 94.0 per cent of the total information of all samples, while the first two encompass 88.8 per cent. Numbers 1 through 11 represent red-soil *P. nelsoni* samples assignable, under criteria previously used, to the subspecies *P. n. nelsoni* and *P. n. discoides*. Samples with relatively wide shells project strongly on the first axis and weakly on the second; the diagonal array of *P. nelsoni* reflects an increase in relative height moving from upper left (number 6 is the type sample of *P. n. discoides*) towards lower right. Samples are evenly spaced along the array and do not cluster into discrete morphological groups. Moreover, samples on the "*discoides*" end of the array are distributed erratically in space and time. The coincidence of morphological clusters with unique spatio-temporal distributions, the criterion by which subspecies were defined in *P. cupula*, does not occur here. Of the four discoides-like samples, number 6 (type *discoides*) is widely separated from its Shore Hills geographic neighbors (numbers 1–5); 8 and 9 are from the opposite western end of Bermuda and 10 (Pl. 2, fig. 2) is one of the two St. George's samples (the other being number 11, most "intermediate" of the red-soil *P. nelsoni*). We have either a polytopic subspecies or

[1] In no other taxon of *Poecilozonites* is there as much infraspecific variation in band onsets and widths within a single pattern. Among red soil samples, only Ireland Island and Cambridge Beaches (localities 65 and 97) do not exhibit the 123 pattern; these lack the upper band and are coded 023. This is particularly intriguing because these samples are the only red-soil *P. nelsoni* from western Bermuda. *P. bermudensis*, discussed in the next chapter, has the same geographic distribution of color: all eastern samples are 123; all western, 023. I do not have enough *P. nelsoni* samples to tell whether the distributions are exactly alike, nor can I pick a preferred hypothesis among the several possibilities of sheer coincidence, similar selective pressures in isolated environments, genetic interchange between the two species, etc.

[2] Non-standarized variables are considered at 40 mm height plus width. Two important samples could not be included in this plot because the sample range in size was insufficient to construct meaningful regressions for predicting values of non-standardized variables at 40 mm. As paratype material belonging to other museums, the shells of these samples (type localities of *P. n. conoides* and "*P. n. gulickiana*"), all of large size, could not be broken back to produce the required size range.

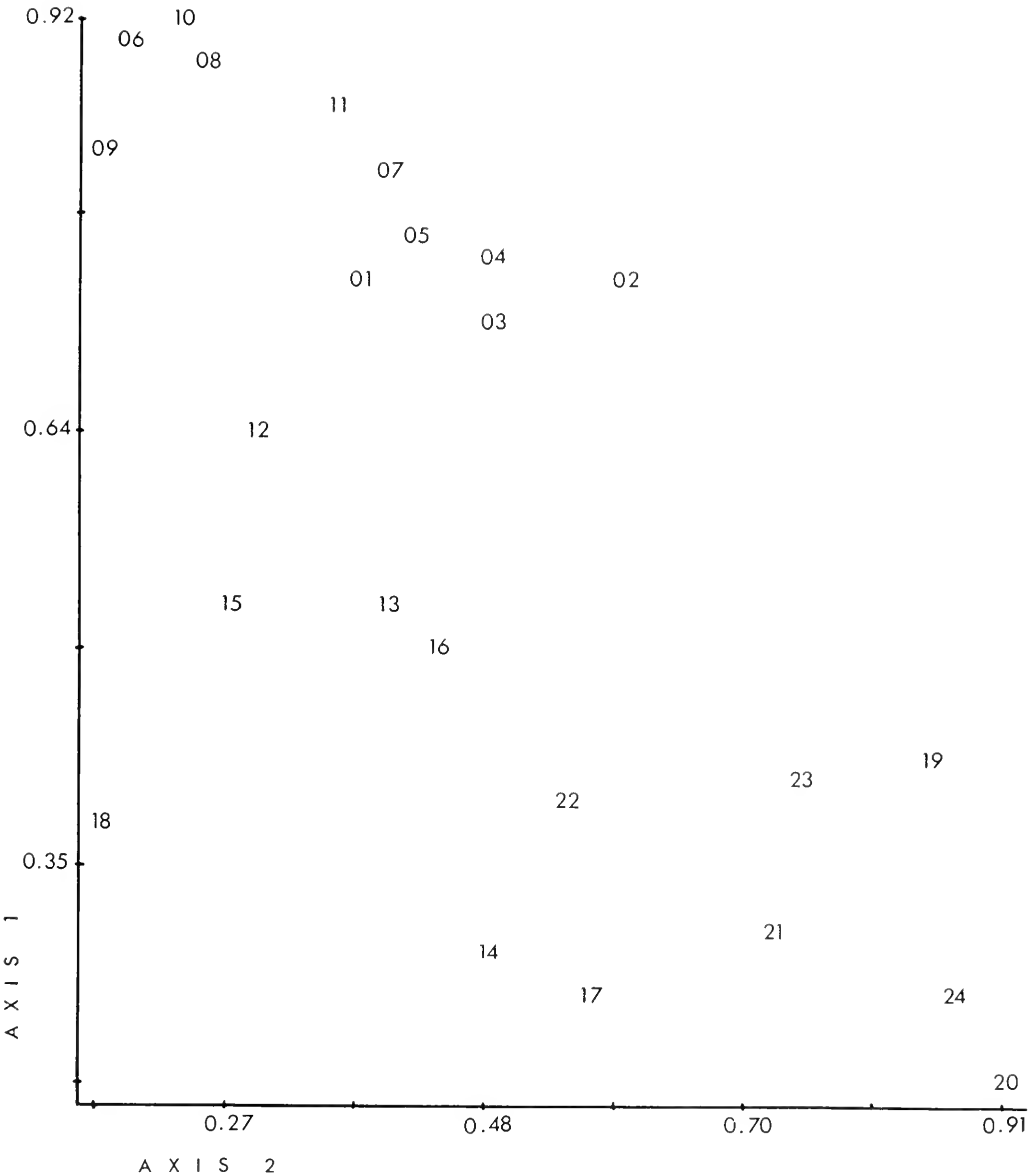

Figure 14. Plot on varimax axes of all samples of the *P. nelsoni* stack. *P.n. nelsoni* (nos. 1–11), *P.n. callosus* (nos. 12–18), *P.s. superior* (nos. 19–20), and *P.s. arenicolus* (nos. 21–24).

a group of samples which have acquired independently a low spire and its set of mechanical consequences (wide umbilicus, relatively wide aperture, etc.). As a character, spire height is so eminently labile that the second alternative seems preferable. The type sample of *P. n. conoides*, likewise, is little more than the highest spired of a morphologically intergrading series of local populations (Pl. 2, figs. 1–5).

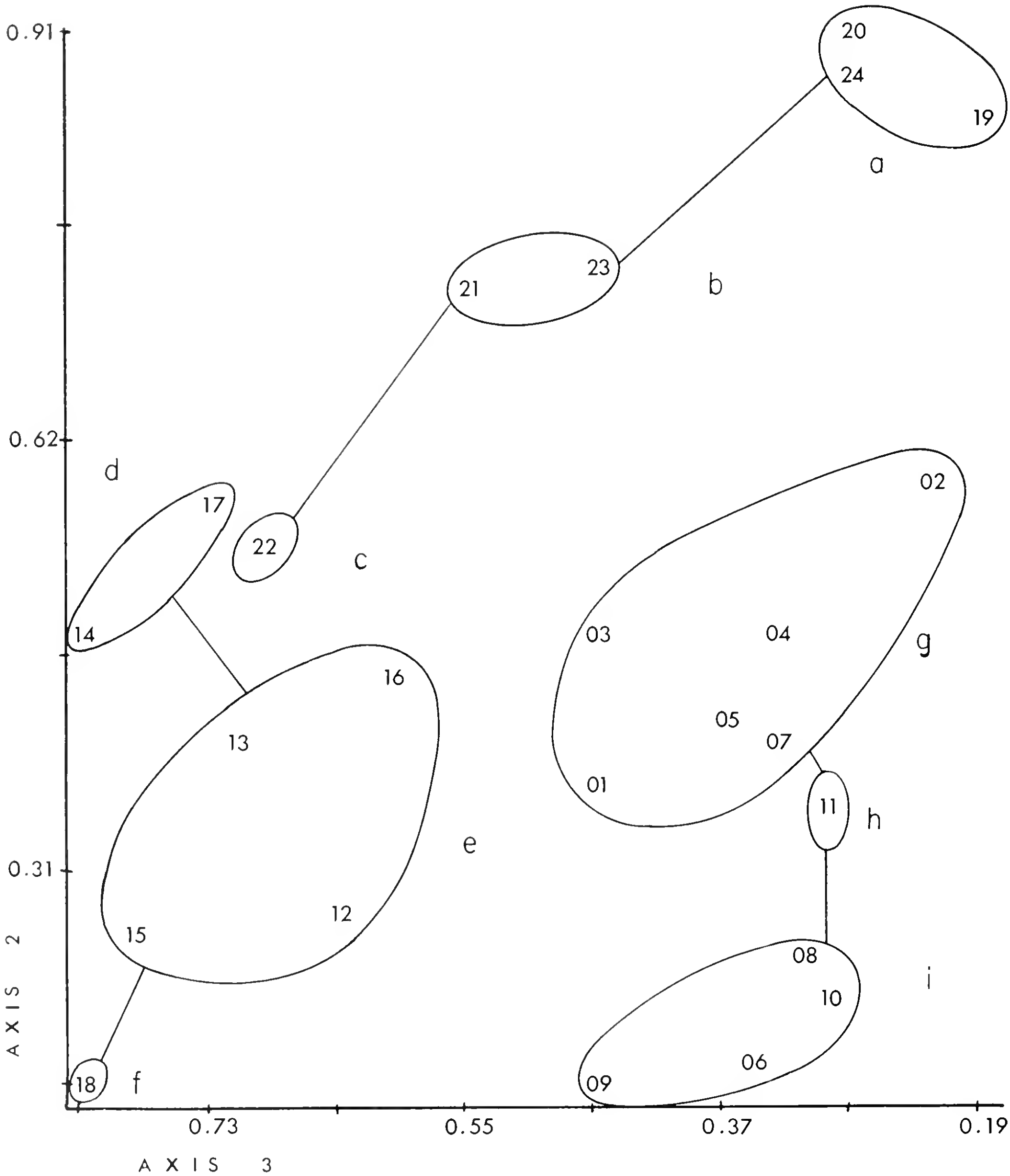

Figure 15. Plot on varimax axes of all samples of the *P. nelsoni* stock. Numbers as in Figure 14. Letters as follows: A, high-spired *P. superior*; B, intermediate *P. superior*; C, low-spired *P. superior*; D, high-spired *P. nelsoni callosus*; E, typical *P. nelsoni callosus*; F, low-spired *P. nelsoni callosus*; G, typical *P. nelsoni nelsoni*; H, intermediate *P. nelsoni nelsoni*; I, low-spired *P. nelsoni nelsoni*.

Finally, "*P. n. gulickiana*" presents no special singularities; its callus does surpass the other red-soil *P. nelsoni* in thickness, but the sharpness of its carina is exceeded by the Ireland Island specimens, the angularity of its aperture by Government Quarry Main Fissure shells, and the weakness of its 1f23 coloration by the type *discoides* and Government Quarry Coquina Fissure samples. To establish subspecies of red-soil *P. nelsoni*, we would need both morphologically discrete sample groups and a geographic distribution linking distinct shapes to non-overlapping geographic areas. Neither of these conditions is fulfilled, and I propose that *P. n. discoides*, *P. n. conoides*, and *P. n. gulickiana* be synonymized with Bland's *P. n. nelsoni*.

This, however, is not the complete story of red-soil samples. Found with normal *P. nelsoni* shells in the Bird Fissure of Government Quarry is a group of specimens whose clear morphological distinction is beyond doubt. (The bimodality for size at the fifth whorl is shown in Figure 16.) Although resembling *P. nelsoni* more than any other taxon of the genus, these specimens share a large set of non-redundant characters unknown in red-soil *P. nelsoni* samples—small final size and small size at a whorl, small protoconch, relatively high spire, high differential growth ratio, and 123 coloration with sharp band margins and no tendency for band fusion. This sample, number 20 of Figures 14–15, projects very weakly on the first axis and most strongly upon the second, which serves as a reference for small, high-spired shells. Of the various causes of bimodality at a locality, sex can be excluded for these hermaphrodites. Age cannot be invoked, because the two groups are distinct not only at their final sizes but also at comparable sizes and whorl numbers (Figs. 14–15, of course, treat all samples at a standardized size). *Post mortem* transport seems unlikely for these exquisitely preserved specimens. Moreover, I have never seen evidence of extensive mixing in any

Figure 16. Histogram of size at fifth whorl for all *P.* (*Poecilozonites*) found in Bird Fissure, Government Quarry. Dotted specimens are *P.n. nelsoni*, blank *P.s. superior.*

of the numerous Shore Hills fissure fills of this area. Several species may occur in the fill, but the shells of any one always possess the morphological coherence of a single local population. We seem, indeed, to be dealing here with two distinct sympatric taxa, i. e. with two species. This conclusion is affirmed by two additional discoveries. By the summer of 1967, Bird Fissure had been blasted away and a new one (or branch of Bird Fissure) opened nearby. The new fauna is identical to that of Bird Fissure—the cahow *Pteroderma cahow*, the distinctive crane *Baeopteryx latipes*, the widely umbilicate *P. nelsoni*, and high spired shells of the new species. I measured the protoconch width of all snails; those of *P. nelsoni* and the new species are distinct at any commonly used significance level ($t = 10.69$ at 56 degrees of freedom). Moreover, a fissure on the south wall of nearby Wilkinson's Quarry locality 34) contains fragments of *P. nelsoni*, several of the small high-spired snails (number 19 of Figs. 14–15) and, again, the crane *B. latipes*. These, in fact, are the only known occurrences of *B. latipes*. The fissure fills of the Walsingham district span a glacial epoch, but individual fissures probably filled rather quickly. In these three fissures, we seem to pick up traces of a unified fauna that inhabited the area for a short duration of the total span. At this time, two large species of *Poecilozonites* lived together in the area. For the

smaller, higher-spired form, I propose the name *Poecilozonites superior* in reference to the elevated spire. (The two species of Bird Fissure are shown in Pl. 2, figs. 7 and 8; formal descriptions will be found in the first appendix.)

In conclusion, two species of large *Poecilozonites* lived in Shore Hills red soils (*P. superior* is unknown from the St. George's). All names previously proposed for red-soil *P. nelsoni* samples are synonymous with *P. n. nelsoni* itself. Non-morphological data were needed to eliminate these superfluous subspecies, for shells shaped appropriately for inclusion under any one of them do not possess the geographic distribution required of biological subspecies. Likewise, sympatric occurrence of *P. nelsoni* and *P. superior* led to their definition as separate species. Thus, both non-morphological criteria of page 460 were usd to establish a classification sufficiently consistent with population structure to permit, or at least not to hamper, an evolutionary interpretation of these taxa.

3. *The P. nelsoni stock in eolianites.* Shells from the *P. n. callosus* type locality, a sand pit of presumed Harrington-Pembroke age, are similar to *P. n. nelsoni* in general shape (Pl. 3, fig. 2), but differ from all red-soil samples in several ways: they are smaller in maximum size and smaller at standardized sizes (from protoconch width to size at the seventh whorl); the shell is thickened (leading to a restricted umbilicus) with a strong callus on the parietal portion of the aperture; the color pattern is, invariably, 023. A number of other Harrington-Pembroke samples share this set of features (numbers 12–18 of figs. 14–15), though each has distinguishing characters that render it unique: the North Shore Road sample (No. 12) is larger-at-a-whorl than all others and therefore projects most strongly upon axis 1, which serves as a reference for large, red-soil *P. nelsoni*. The samples from Sayles's type locality of the Harrington Formation[1] (numbers 14 and 17, and Pl. 3, fig. 1) surpass the others in relative height and project strongly upon axis 2 (the reference for high-spired Shore-Hills *P. superior*). The low-spired St. David's Island shells (number 18 and Pl. 3, fig. 3) are remarkably thick and heavily callused (and have a *wide* umbilicus despite the usual negative correlation of shell thickness and umbilical width). Thus, the validity of Gulick's *P. nelsoni callosus* is affirmed, not from its morphological uniqueness alone, but because it, unlike the rejected subspecies of Gulick, Verrill and Pilsbry, occupies a distinct spatio-temporal segment of the species range.

The Harrington-Pembroke formations contain yet another group of samples. These (numbers 21–24 of Figs. 14–15) are high spired, lack a strong callus (despite shell thickness equal to that of *P. n. callosus*) and, especially, exhibit color patterns 103 or $12^{n}3$ (band 2 is always well developed in *P. n. callosus*, band 1 always absent). Although they have never been found together in the same outcrop, the range of these samples is coextensive with that of *P. n. callosus.* This implication of sympatry and tendency toward high spires suggests that these samples are a subspecies of *P. superior*, here named *P. superior arenicolus* in reference to its dune habitat (Pl. 3, figs. 4 and 5).

When all samples of the *P. nelsoni* stock are considered, we can delimit three major morphologies: the large, thinly callused, relatively low-spired *P. n. nelsoni;* the small, thickly callused, relatively low-spired

[1] I collected number 14 at Sayles type Harrington, but found number 17 in the Sayles collection at Antioch College, labelled simply "South Shore Harrington Sound"—an area including the type Harrington but not excluding other exposures. That the two are drawn from the same local population (and probably come from the same exposure) is indicated by their close similarity as measured by all variables. They appear closely together on all varimax plots.

P. n. callosus; and the small, thinly callused, relatively high-spired *P. superior superior* and *P. s. arenicolus.* The first three varimax axes (94.0 per cent of the total information) encompass these three trends in form. *P. n. nelsoni* samples sort with the first axis, the largest and lowest spired samples doing so most strongly. The second axis is a reference for *P. superior;* the highest projection on this axis is that of the smallest and highest-spired sample, the Bird Fissure *P. s. superior.* Grouping with the third axis (Fig. 15) are shells of *P. n. callosus:* the St. David's Island sample, smallest, lowest-spired, and most strongly callused of *P. n. callosus* samples, projects most strongly on this axis. When each sample is grouped with the oblique axis upon which it projects most strongly (Table 10), virtually complete discrimination of the taxa is obtained. Of 24 samples, only one is misallocated; the Trunk Island sample of *P. s. arenicolus* (number 22 of Figs. 14 and 15), lowest spired of its species, groups with the *P. n. callosus* samples.

Of course, each taxon must be seen not as if glued to a set of distinctive characters, but rather as operating in a reaction range that does not include the total form spectrum of the entire stock. Overlap will occur where the ranges intersect. Were it not for differences in color and callus, the lowest-spired *P. s. arenicolus* (number 22) might not be distinguished from the highest-spired sample of *P. n. callosus* (numbers 14 and 17). One genetic difference between *P. nelsoni* and *P. superior* lies, presumably, in the ability of the former species to produce a callus. This potential is translated to morphology in eolianite environments (carbonate dunes), where lime sufficient for its production is available. Samples of the two species in this environment can be distinguished thereby. In calcium-poor red soils, the potential remains that alone and, in the further absence of firm color distinctions, allocation of a sample to its proper species is difficult in certain cases. I have found no way to tell, for example, whether the single magnificent specimen from a small fissure on Harrington Sound Road (Pl. 2, fig. 5) is an exceptionally high-spired *P. n. nelsoni* or a large *P. s. superior.*

TABLE 10. OBLIQUE PROJECTION MATRIX FOR ALL SAMPLES OF THE *P. NELSONI* COMPLEX. The following identifying information is given for each sample: trivial name of the subspecies, locality number and age (SH = Shore Hills, HP = Harrington-Pembroke, SC = St. George's).

Sample			Axis 1	Axis 2	Axis 3
nelsoni	18	SC	1.000	0.000	0.000
nelsoni	65	SH	0.969	0.050	0.033
nelsoni	P2	SH	0.946	−0.068	0.114
nelsoni	68	SC	0.921	0.199	−0.018
nelsoni	30	SH	0.853	0.263	0.008
nelsoni	5B	SH	0.796	0.506	−0.172
nelsoni	97	SH	0.785	−0.083	0.312
nelsoni	89	SH	0.779	0.366	0.004
nelsoni	P9	SH	0.770	0.283	0.094
nelsoni	5M	SH	0.682	0.244	0.234
nelsoni	5C	SH	0.599	0.332	0.246
superior	5B	SH	0.000	1.000	0.000
arenicolus	?	HP	0.090	0.970	−0.019
superior	34	SH	0.348	0.888	−0.173
arenicolus	11	HP	0.200	0.737	0.237
arenicolus	63	HP	0.007	0.730	0.422
callosus	84	HP	0.000	0.000	1.000
callosus	45	HP	−0.137	0.406	0.896
callosus	86	HP	0.182	0.077	0.861
callosus	?45	HP	−0.149	0.546	0.766
callosus	30	HP	0.242	0.277	0.678
arenicolus	100	HP	0.055	0.474	0.657
callosus	95	HP	0.462	0.139	0.559
callosus	P8	HP	0.270	0.382	0.518

C) *Mode and Significance of Temporal Changes in Morphology*

The most satisfying aspect of observed morphological differences between red-soil and eolianite samples is the availability of a reasonable adaptive explanation. Such explanation is particularly welcome in pulmonates, since it has been claimed so often that patterns in diversity bear no

relationship to environment in this group.[1] The three features which distinguish virtually all eolianite samples from all red-soil shells are the smaller size (absolutely and at a whorl), the thicker shell, and the weaker coloration (023, 103 or $12^{n}3$ with a tendency for narrower bands of lighter color—this lightness, however, may be a preservation artifact—compared with the generally wide and dark bands of the red-soil 123 pattern). (The fourth feature, a narrower umbilicus, is a consequence of restriction by shell thickening in *P. n. callosus* or by thickening and increasing relative height in *P. s. arenicolus.*)

The relationship of size and environment is obscure, though Rensch (1932) has suggested that the absence of dry spells produces larger shells by reducing the percentage of lifetime spent in estivation. Bermuda was wetter during glacial (red-soil) periods (see Chapter 9). The weaker coloration can be explained in two ways. Rensch (1932) found a strong positive correlation between increasing mean intensity of solar illumination and weaker coloration; the whiter the outer shell layer, the more reflective of light. The white dunes must have received more illumination than thickly vegetated soils of the wetter glacial periods. Alternately, the weak coloration of eolianite snails may have been cryptic. I suspect that the white dunes were sparsely vegetated, as are the modern dunes of Elbow Beach and Tuckerstown. The red soils were not only deeply colored in themselves, but also mantled in vegetation if today's situation is representative (Bermuda's agriculture is centered on exposures of the fossil red soils).

Differences in shell thickness are most easily explained. It has been shown again and again (see Chapter 9) that land snails extract lime for their shells from the rocks upon which they live (viz. the abundance of pulmonates on many limestone outcrops). Normally thick-shelled species produce paper thin shells (if they survive at all) when deprived of calcium carbonate (Oldham, 1934, Rensch, 1932). The eolianites are all carbonate, while $CaCO_3$ constitutes less than 2 per cent of some red soils (Ruhe, et al., 1961). Shell thickening and loss of color are attained in two different ways in two independent taxa. Such multiple solutions may be taken to indicate the adaptive necessity of these modifications.

One final question must be posed: Did the eolianite subspecies evolve directly from Shore Hills progenitors (and then back again to produce the St. George's *P. n. nelsoni*—see Henningsmoen, 1964, on zigzag evolution), or did two subspecies of each species persist in different areas and environments from, at least, Shore Hills through Pembroke time. As is usual in paleontology, the literal interpretation of zigzag evolution is less likely. The two subspecies of each species are distinguished by a large set of characters, not all of which can be presently seen as subject to precise and necessary expression in given environments. Thus, we would expect a St. George's derivate of *P. n. callosus* to reacquire the thin shell and strong coloration of the Shore Hills *P. n. nelsoni,* but we would not anticipate so precise a return to previous morphologies. This, however, is not the strongest argument.

Bermudian stratigraphy is a complex of facies, not a layer cake. Throughout the Pleistocene, dunes formed at the periphery of the islands and became cemented before they could migrate inland (Bretz, 1960; Land, Mackenzie, and Gould, 1967); red soils formed in sheltered central parts. During glacial times, the island periphery stood several miles out and a few hundred

[1] This debate is discussed in Chapter 9 which treats, in much greater detail, the whole question of climate and evolution in land snails. This chapter should be consulted for the documentation of statements cited here without evidence, e.g. of the contention that shell thickness is related to the availability of calcium carbonate in the environment.

feet below present sea level. Of dunes formed in glacial times, only North Rock, a small pinnacle ten miles off Bermuda's north shore, remains awash. A vertical sequence of red soil-eolianite-red soil therefore reflects the migration of environments in response to shifts in sea level. The corresponding faunal sequence, *P. n. nelsoni-P. n. callosus-P. n. nelsoni* need not represent evolution *in situ* but is, more likely, the fragmentary record at one point in space of the fact that two subspecies, each tied to a particular environment (hence to a particular geographic domain), lived through the time of the entire sedimentary sequence. (This possibility, by the way, was the basis of Newell's argument that the "chronological subspecies" is not necessarily an artifact of convenience having no relation to its biological counterpart of local races occupying a geographic subsection of the species range—Newell, 1947). The first possibility, zigzag evolution, carries the implication that a given environment elicits a definite morphological response (which may be phenotypic only) in all cases. The second, that of well-defined, long-ranging subspecies, suggests that each subspecies is a distinct genetic entity (still capable of interbreeding with others, of course). Hence, even if an occasional local population survives in the "alien" environment, it will not alter in form to identity with the usual subspecies of that environment, but will retain enough of its features to be recognizable. I find it a most convincing test of this second possibility that such local populations have twice been found in Bermuda:

1. In an eolianite of Harrington age exposed on South Shore Road at Saucos Hill (locality 64): a few specimens clearly assignable to *P. n. nelsoni* (large protoconch, strong 123 coloration—see matrix of means in appendix). The two preserved calluses are thicker than those of any other *P. n. nelsoni.* Shell thickness, if a simple function of the availability of lime, will alter in immediate phenotypic response to this factor.

2. In the Shore Hills soil at Ferry Road, north of the Biostation locality 11: four shells which, in their high spire and 12"3 coloration with sharp band margins, possess the distinguishing characters of *P. s. arenicolus.* These are, however, thin-shelled, demonstrating once again the response of shell thickness to environment of deposition.

I conclude that the *P. nelsoni* stock, as known today, consists of two closely-related species; each of these is, in turn, divisible into two subspecies, one adapted to red soils, the other to eolianites. These two environments persisted throughout the Bermudian Pleistocene, migrating back and forth across the platform in response to fluctuating sea levels of the ice age. The subspecies migrated with the environments and a vertical sequence, though giving the appearance of zigzag evolution, merely reflects the view of a static observer who spent the Pleistocene watching the march of environments at his single station.

VIII. PHYLETIC BRANCHING IN THE *P. BERMUDENSIS ZONATUS* STOCK

A) Introduction

Of the four species of *P.* (*Poecilozonites*), *P. bermudensis* is most abundant by far as a fossil; shells are plentiful and well preserved in all post-Belmont formations. In addition, *P. bermudensis bermudensis* is the only living representative of the subgenus. The high precision of temporal and geographic control and the existence of a living form combine to make this species a particularly favorable object of evolutionary investigation. During the last 300,000 years, the central stock of the species, *P. bermudensis zonatus* Verrill 1902, has branched at least four times and has itself undergone fluctuating alterations of morphology that correlate with ice age climatic oscillations. Illustrated here are the two major evolutionary events of phy-

logeny: speciation or the multiplication of lineages and phyletic evolution or the transformation of lineages. In our microcosm, branches may not reach the specific level of distinction, and patterns of transformation may involve phenotypic modification with little genetic basis; yet the two modes are illustrated, even if in miniature. Branching of the *P. bermudensis zonatus* stock will be considered in this chapter, its phyletic transformations in the next.

Diversity of form and color among samples of *P. bermudensis* is far less pronounced than in *P. cupula*. Whereas a single well-preserved *P. cupula* shell can be identified unambiguously as belonging to one of its 13 local populations, local distinction of *P. bermudensis* is not nearly so strong; if given a single *P. bermudensis zonatus* shell, I can distinguish only between Shore Hills and later specimens and between eastern and western Bermuda. An interesting question, and one which will probably never be answered, concerns the cause of this difference in variability. Is it a taxonomic artifact? (Are the *P. cupula* subspecies really species? Is *P. bermudensis* merely a spectacularly successful side branch of the *P. cupula* stock, ranking with the *P. cupula* subspecies in genetic distinctness but given specific status because of its abundance?). Or does it reflect something more fundamental about the genetic background and habitat preferences of *P. bermudensis*?

The lowered variability of form is matched by the stability of color pattern. Only two color types (and their extensive sets of subtypes) are known in *P. bermudensis*, but the geographic distribution of these types is a fundamental datum. East of a line passing through Devonshire Marsh on the north (locality P7) and Cox's Bay (just west of locality 47) on the south, all fossil *P. bermudensis* samples exhibit band pattern 123; 023 occurs west of this line (Pl. 1, figs. 6–7). The margins of band 2 are sharp in the western forms, diffuse in eastern samples. With the exception of a single intermediate sample found by Haycock in Devonshire Marsh,[1] the distinction is as clear near the area of potential contact as at opposite ends of the island. I assume that genetic exchange between eastern and western snails was eliminated or greatly curtailed during the whole Shore Hills-Southampton interval and that *P. bermudensis zonatus* was evolving as two parallel stocks during that time. At some time after the end of Southampton deposition, *P. bermudensis zonatus* became extinct. Its primary range on the main island was quickly repopulated by *P. bermudensis bermudensis*, which had been evolving in isolation on St. George's Island since St. George's time;[2] the color pattern of all modern snails is therefore 123.

Another variation in color pattern is unique to *P. bermudensis*. In all post-Shore Hills samples of *P. bermudensis zonatus* from eastern Bermuda, a number of large shells (from 5 per cent to 80 per cent of the total collection) develop apparently normal bands, which are replaced during ontogeny by diffuse lines of color at the previous band peripheries (Pl. 5, fig. 5). The time of onset of this phenomenon, which I shall call "faded," varies but

[1] Haycock collection, Bermuda Museum. I cannot exclude the possibility that this sample is mixed or mislabelled. The locality is now a garbage dump.

[2] This extinction, completely undocumented in the preserved record, is itself one of the most fascinating events in the history of *P. bermudensis*. Since it occurred after the latest deposition of Southampton dunes, the extinction is a very recent event, probably attributable to human disruption of the native biota. Isolated on St. George's Island, *P. bermudensis bermudensis* survived the plagues of rats, pigs, and snails that ravaged Bermuda during the early settlements (see Chapter 2) and later repopulated the whole island complex. That a few hundred years is adequate time for such a colonization (especially with the aid of human ferrying) is indicated by the work of Crampton (1916, 1925, 1932) on rapid migrations in *Partula*.

usually occurs between the fourth and fifth whorl. In samples from western Bermuda, the "faded" characteristic is either absent or present at low frequency (invariably less than 10 per cent).

B) The Branching Occurs by Paedomorphosis

The exception to the statement that *P. bermudensis* displays little diversity is provided by a group of samples which share common attributes not occurring in *P. bermudensis zonatus*. These samples occur in four discontinuous segments of the space-time framework:[1]

1. In the Shore Hills Soil exposed in caves north of Tom Moore's Tavern (locality 53), *P. b. fasolti* new subsp. (Pl. 4, fig. 3).

2. In the Harrington Formation at two localities on the southern tip of Ireland Island (locality 10), *P. b. siegmundi* new subsp. (Pl. 4, fig. 4).

3. In the Harrington and lowest Pembroke Formations at Rocky Bay (locality 44), *P. b. sieglindae* new subsp. (Pl. 4, fig. 5).

4. In the St. George's and Southampton Formations on St. George's Island, spreading to the main island after the extinction of *P. bermudensis zonatus* in recent time (localities 11, 12, 15, 16, 19, 21, 24, 27 for St. George's and Southampton fossils and 78, 79, 80, 81, 82, 83, 88 for living populations), *P. b. bermudensis* (Pfeiffer) (Pl. 5, fig. 6).

These samples are distinct from *P. bermudensis zonatus* in the following ways (non-standardized measures considered at height + width = 30 mm in all subspecies; see matrix of means, Appendix 3, for numerical comparisons and Pl. 4 for photographs):

1. Color is considerably less intense. This effect is most pronounced in *P. b. fasolti* and St. George's-Southampton samples of *P. b. bermudensis*. In shells of these populations, flames are invariably present in band positions 1 and 2; even band 3, which always forms by the third whorl in *P. b. zonatus*, may be undeveloped, its area occupied by closely spaced flames.

2. The shell is relatively much thinner.

3. The parietal callus is completely absent (*P. b. fasolti*, *P. b. bermudensis*) or very weakly developed (*P. b. siegmundi*, *P. b. sieglindae*).

4. The spire is relatively lower; a larger percentage of the total height is accounted for by apertural height.

5. The shell is relatively wider.

6. The differential growth ratio is lower.

7. The aperture is relatively wider.

8. The umbilicus is wider.

9. The cross-sectional profile of the dome is smoother.

10. The lowest point of the subperipheral portion of the outer apertural lip is closer to the umbilicus.

A comparison of this list with the tabulation of allometric trends in ontogeny (Chapter 4) demonstrates that, for eight of ten points, these samples possess at large sizes features which characterize earlier ontogenetic stages of *P. bermudensis zonatus*. The two exceptions are readily resolved into the general interpretation.

a) After reaching an early maximum, umbilical width remains constant during ontogeny. Umbilical width is a mechanical correlate of relative shell width at the point in growth at which umbilical width becomes maximal. The differential growth ratio, although lowered in these samples, is still considerably greater than 1, and relative height of the post-embryonic spire increases continually during growth. Since relative height at 30 mm is a good deal less in these samples than in *P. bermudensis zonatus*, relative width at the point of maximal umbilical width will likewise be greater than relative width at the corresponding point in *P. bermudensis zonatus*.

[1] Although the justification for separate subspecific status will be presented in section C, the names are introduced here to facilitate referencing in discussion.

Hence, the umbilicus of these samples will be absolutely wider.

b) The differential growth ratio is constant during the growth of an individual. The power function applies from the termination of whorl 2 to the end of growth. From hatching to the end of whorl 2, growth in relative width is remarkably rapid, transforming the quadrate protoconch (Pl. 3, fig. 6) into a disk-like juvenile. The differential growth ratio is low at first, increasing gradually until its value becomes stabilized. Lowered differential growth ratio can be interpreted as a retention of juvenile growth rates.

The mere enumeration of a list of differences is worth little without an assessment of redundancy among its items, for all entries in an impressive tabulation may measure a single dimension of variation.

Not all the 10 components of the foregoing list are independent. The low spire is produced by a low differential growth ratio and implies, in turn, a relatively wide aperture. A shell with a low spire and relatively wide aperture will be relatively wide in general, from which the production of an absolutely wide umbilicus can be inferred. Items 4 through 8 measure only one aspect of variation. When the redundancies are eliminated, however, there remain at least four groups of variables which, in 8-axis oblique factor solutions (see Chapter 5), generally sort separately. These are:

a) measures of color (item 1)

b) the callus (item 3)

c) measures of form ratio (items 4–8)

d) conformation of the subperipheral portion of the outer apertural lip (item 10).

To say that there are at least four separate dimensions of variation in the list is not to assert that the four are unrelated. All are linked in ontogeny, since small shells of *P. b. zonatus* are weakly colored, lack a callus, are relatively wide, and have the lowest portion of the outer apertural lip at the umbilical border (Pl. 4, fig. 2). It is certainly a significant datum that a group of traits which normally occur together in juvenile shells of an ancestor maintain their association and reach the same values at maximal sizes in descendants. This can be interpreted in only one way—the subspecies are paedomorphic branches of the central stock, *P. bermudensis zonatus*. *Every* characteristic ontogenetic feature developed at or after the fifth whorl in these subspecies is attained by whorl 3–4 in *P. bermudensis zonatus*.

Two objections often raised to hypotheses of paedomorphosis are either invalid or inapplicable to this case:

a) Paedomorphosis has been proposed to explain the presence in adult descendants of one or a small group of features that typify earlier stages of ancestral ontogeny. That the hair distribution of human adults is similar to that of fetal chimpanzees need not imply that hair loss in human evolution occurred by embryonic retention, but rather that less hairy individuals were selected from the static spectrum of variation at adult sizes. This will not apply to the large specimens of these paedomorphic subspecies, which are scaled-up replicas of earlier stages in the ontogeny of *P. bermudensis zonatus* (Pl. 4, fig. 2 and figs. 3–6). Whereas the similarity in shape between a single trait of a young ancestor and adult descendant can easily be attributed to coincidence, the probability that such an explanation could apply to every measurable feature of ontogeny is effectively nil.

b) By a curious *non sequitur*, the citation of adaptive significance for an evolutionary change has been judged a denial of paedomorphosis as the mode of alteration. Paedomorphosis, is, in de Beer's phrase (1958: 36), a "morphological mode" by which selection can operate to produce adaptive adult configurations. If a thin shell, weak coloration, relatively wide shell, or any combination of these was favored by selection, paedomorphosis is one mode

among many by which the change could have been effected.

C) Paedomorphosis Occurred at Least Four Times

The proposition that two taxa, one a paedomorphic derivative of the other, inhabited Bermuda during the Shore Hills-Southampton interval is the simplest phyletic interpretation that can be given to the distribution of paedomorphic samples; this interpretation is implicit in earlier work. Gulick (1904) and Verrill (1905) realized that fossil and modern *P. bermudensis* were distinguishable, and assumed a simple unilinear derivation, since they did not find paedomorphic fossils. Gulick even recognized, for the wrong reasons, that modern shells resembled earlier ontogenetic stages of fossil forms: "Thus in their smaller number of whorls [this is not true], their less rounded contour [by which he means less strongly domed, not rougher in cross-sectional outline], and their [relatively] larger umbilicus, the present snails seem like an undeveloped or degenerate race of the former species" (Gulick, 1904: 419). As paedomorphic fossils were discovered, the notion that two closely related species persisted throughout the preserved Pleistocene sequence gained favor: Peile (1926) listed *P. zonatus* and *P. bermudensis* in his synopsis of the subgenus.

I found a more complex story, involving an unusually literal interpretation of paleontological data. Each of the four discontinuous occurrences represents an independent episode of paedomorphosis. Evidence for separate origins will be presented with reference to Figures 17–19, Q-mode plots for all measured samples of *P. bermudensis.* Numbers on these plots correspond to the following samples:

a) Shore Hills non-paedomorphs: 01, 02, 02, 04

b) Shore Hills paedomorph (*P. b. fasolti*): 05

c) Harrington non-paedomorphs: 06, 07, 08, 09, 10

d) Harrington paedomorphs (*P. b. sieglindae, P. b. siegmundi*): 12, 13

e) Pembroke non-paedomorphs: 11, 14, 15, 16

f) Pembroke paedomorph (*P. b. sieglindae*): 17

g) St. George's non-paedomorphs: 18, 19, 20, 21, 22

h) St. George's paedomorph (*P. b. bermudensis*): 23

i) Southampton non-paedomorphs: 24, 25, 26, 27

j) Southampton paedomorphs (*P. b. bermudensis*): 28, 29, 30

k) Recent paedomorphs (*P. b. bermudensis*): 31, 32, 33, 34, 35, 36.

The Shore Hills paedomorph shares with other samples of its geologic formation those unique morphological features that separate these oldest *P. bermudensis* samples from all others. Shore Hills shells are distinguished by their small size at a whorl,[1] their remarkably flattened apex (measured by the initial form index), and low values of the lower eccentricity (Table 11 and Chapter 4 for definition of measures). Other morphological consequences ensue: the flat apex produces a low spire, a relatively wide shell, and a wide umbilicus. Shore Hills samples of *P. b. zonatus* are maximal among non-paedomorphs in umbilical widths; *P. b. fasolti* exceeds all other paedomorphs in this measure. Shore Hills *P. b. zonatus* are relatively widest among non-paedomorphs at the fifth whorl; *P. b. fasolti* surpasses all other paedomorphs in relative width. The lower eccentricity of Shore Hills *P. b. zonatus* is lower than that of all more recent non-paedomorphs; no post-Shore Hills paedo-

[1] This serves to emphasize the fact that large whorl size does not imply large maximal size. Shore Hills shells grow to absolutely larger sizes than all more recent *P. bermudensis*, despite their smallest size at a whorl—i.e., they have more whorls at maximum sizes.

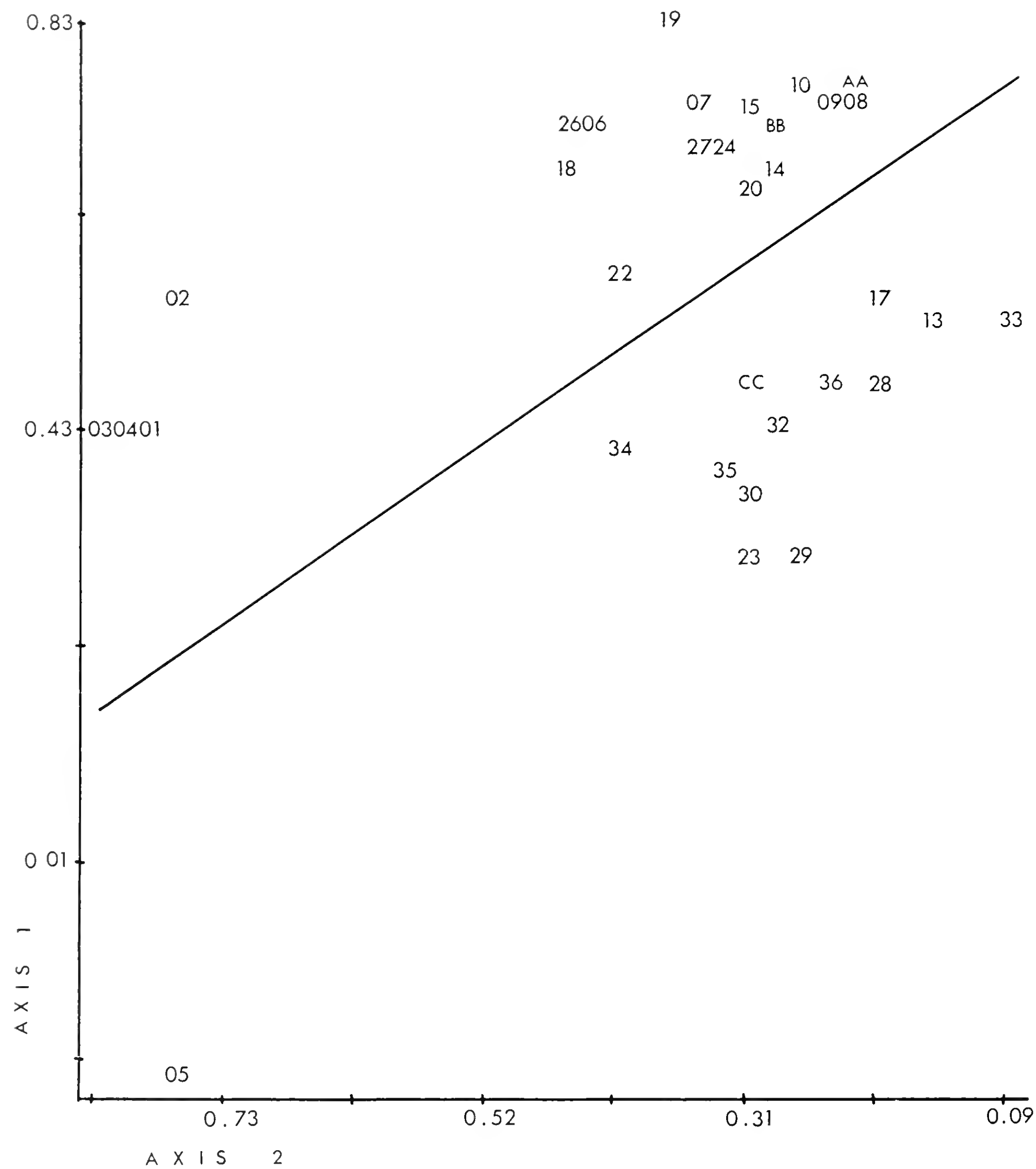

Figure 17. Plot on varimax axes of all *P. bermudensis* samples. AA stands for 11 and 21, BB for 16 and 25, CC for 12 and 31. Diagonal line separates all non-paedomorphs (above) from all paedomorphs (below).

morph attains a value of this variable as low as that of *P. b. fasolti* (etc. for the entire set of features distinguishing paedomorphs from non-paedomorphs). The extent of the morphological gap separating Shore Hills from later samples is evident in Figure 17. (The arbitrary oblique line of this figure divides paedomorphs from non-paedomorphs; note the distance between *P. b. fasolti* and the other three paedomorphic subspecies.)

The postulate that Harrington paedo-

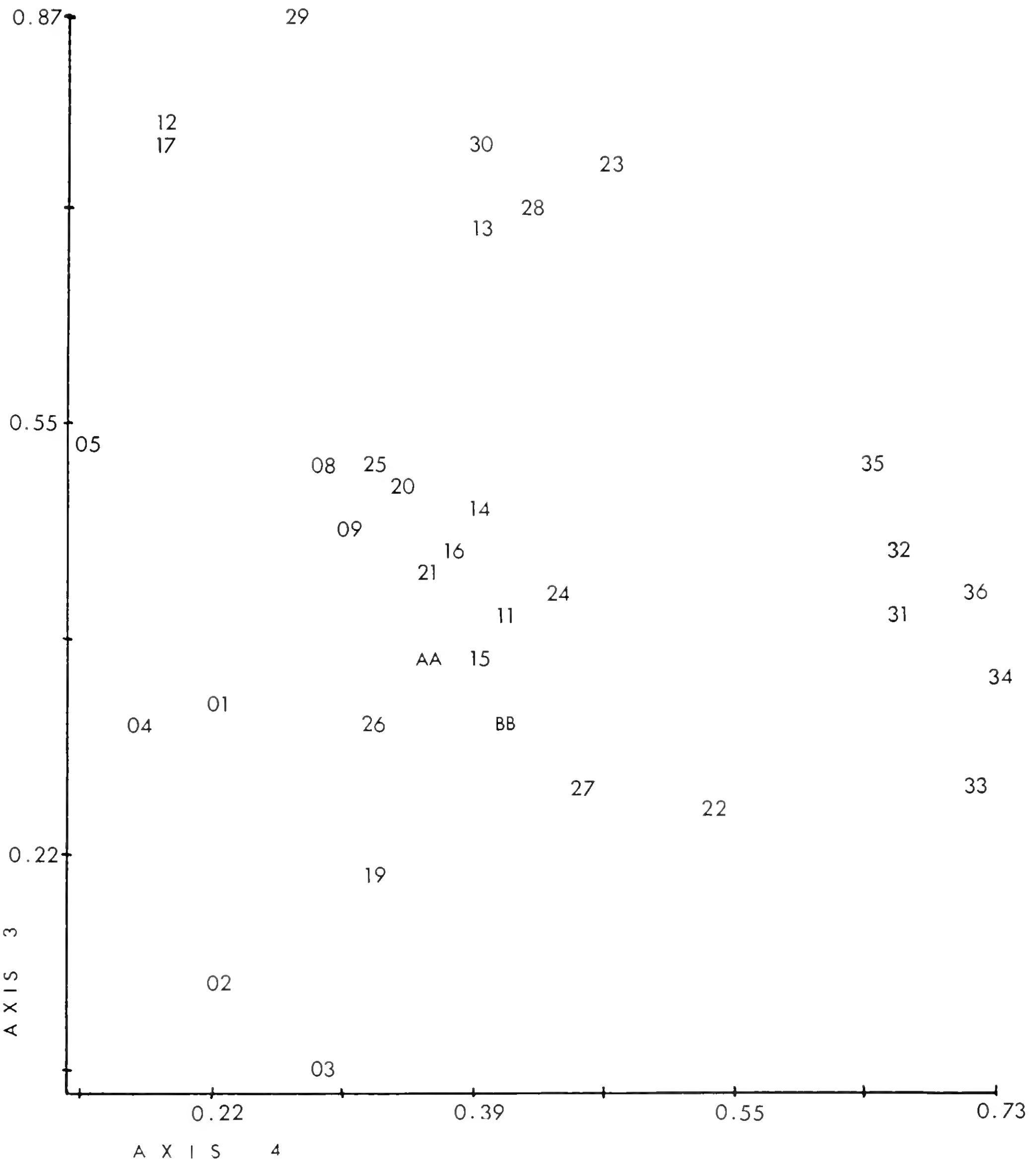

Figure 18. Plot on varimax axes of all *P. bermudensis* samples. Fourth axis separates modern *P.b. bermudensis* (31–36) from all other paedomorphs. AA stands for 07 and 10, BB for 16 and 18.

morphs evolved directly from *P. b. fasolti* involves the improbable hypothesis that the unique features of Shore Hills samples were modified twice in exactly the same manner. The parallel modification of large numbers of variables is not in itself improbable and must occur if paedomorphosis in *P. bermudensis* is recurrent, as proposed here. Frequent development of the many traits characterizing paedomorphic shells

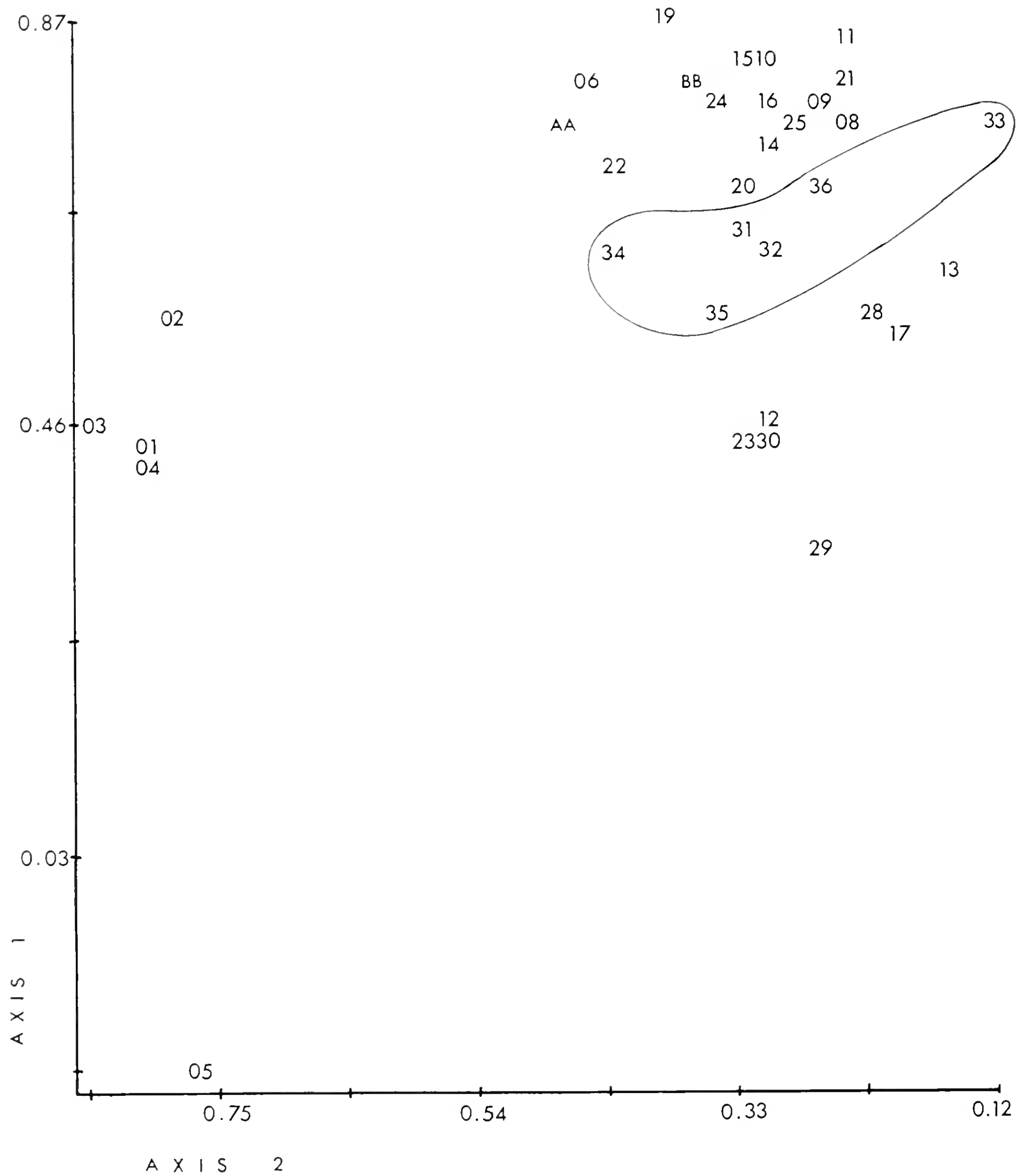

Figure 19. Plot of all *P. bermudensis* samples. Modern *P.b. bermudensis* circled; note intermediate position between post-Shore Hills paedomorphs and non-paedomorphs. AA stands for 18 and 26, BB for 07 and 27.

has a potentially simple genetic base, but a double origin of Harrington *P. bermudensis* would involve the similar independent development of many unrelated features. Increase in whorl size will not mechanically produce a more convex spire and, if anything, should bring about a *decrease* of the lower eccentricity, for large shells at a whorl have fewer whorls at the standard size, and the positive correlation

Table 11. *P. bermudensis*: comparison of Shore Hills samples with more recent samples. Figures cited are ranges of mean sample values in mm.

	Shore Hills	More Recent
Size at the fifth whorl	12.85–13.99	14.47–16.77
Initial form index	0.158–0.186	0.207–0.293
Umbilical width:		
paedomorphs	3.01	1.82–2.51
non-paedomorphs	2.22–2.40	1.69–2.22
Lower eccentricity:		
paedomorphs	0.182	0.256–0.446
non-paedomorphs	0.318–0.380	0.425–0.528

of lower eccentricity is stronger with whorl numbers than with size. When all measured features are considered, the Harrington paedomorphs are more similar to Harrington non-paedomorphs than to *P. b. fasolti*, which is best regarded as a short-lived branch derived from Shore Hills *P. bermudensis zonatus* (Fig. 20).

In Harrington times, paedomorphic populations evolved at the range peripheries of eastern and western *P. bermudensis zonatus*. *P. b. siegmundi*, found in two localities on Ireland Island, displays the typical western color pattern—023 with band formation delayed; *P. b. sieglindae*, bearing the 123 pattern, arose at Rocky Bay in the southwest corner of the range of eastern snails. Since eastern and western stocks were evolving separately during the Shore Hills-Southampton interval, the two paedomorphs are independent developments.

Another eastern paedomorph, *P. b. bermudensis*, evolved in St. George's time on what is now St. George's Island in northeast Bermuda. The proposal for an origin of this form separate from that of *P. b. sieglindae* is weaker than previous cases of distinct derivation. Yet I maintain this view for the following reasons:

a) *P. b. bermudensis* evolved at a range periphery of *P. b. zonatus* opposite from the point of origin of *P. b. sieglindae*.

b) *P. b. sieglindae* seems to have been a small, isolated, and short-lived population. It extends only from the uppermost Harrington to the lowest Pembroke and was probably annihilated by the strong growth of Pembroke dunes. In lower Pembroke times, its range is narrowly limited to the east and west by populations of *P. b. zonatus* at localities 2 and 47; the entire east-west extent of its Pembroke range could not have exceeded 200 meters.

I conclude that the *P. bermudensis zonatus* stock branched at least four times during the Shore Hills-St. George's interval, that each branch is a paedomorphic derivative of the central stock, and that an extensive set of similar and non-redundant morphological features therefore evolved many times and independently. This heterochronous parallelism or "iterative evolution"[1] has been documented in other fossil groups. It is best known among Mesozoic ammonoids and in the repetitive development of the ostreid form genus *Gryphaea*. Iterative trends in the evolution of brachiopod lophophores have been documented by Elliott (1948), who cites further cases among echinoids and foraminifera. Standard objections to such hypotheses involve the "complexity" of morphological alteration (usually defined in terms of the number of differences that can be cited) and the improbability of its repetitive occurrence. But complexity is not a matter of simple enumeration; in this case many characters are involved, but the change has a simple genetic and ontogenetic basis—the very prerequisites listed by Simpson (1953: 251) for the occurrence of iterative trends.

Rensch (1937) has provided an interesting analogy that should dispel qualms as to the improbability of independent origin for markedly similar shapes. In western

[1] Simpson's definition (1953: 248) of iterative evolution fits this example particularly well: "The repeated occurrence of similar trends in successive offshoots of a group, often form a continuing 'conservative stem.' "

Sicily are found flattened, carinate, umbilicate subspecies of six genera that are normally smooth, rounded, and non-umbilicate in the manner of such typical helicids as *Otala*. Moreover, "similarity among the carinate races, which have arisen independently in parallel fashion, is so great that, on the basis of the shell alone, *Murella muralis scabriuscula*, *Tyrrheniberus villica sardonia*, and *Rossmaessleria subsc. subscabriuscula* could be considered as races of a single species. Such cases are of great significance for paleontology" (translated from Rensch, 1937: 587). Here similarity among derived subspecies of three genera is stronger than that among the four paedomorphic subspecies of *P. bermudensis*, for only between an uncallused *P. b. sieglindae* and *P. b. bermudensis* could any difficulty of identification arise in well-preserved specimens. The uncanny aspect of Rensch's example is that the passage from rounded, non-carinate forms to sharply keeled derivatives is reminiscent of the transition from *P. b. zonatus* to its paedomorphic branches. Yet it is analogy only, for Rensch's carinate forms are not derived by paedomorphosis and seem for the most part to have thicker shells than typically-shaped subspecies.

The emphasis on simplicity of genetic and ontogenetic production of paedomorphic forms raises another important issue: Granted that the four branches are distinct and paedomorphic, does the change have any genetic basis? Is this case merely another *Ambystoma*-axolotl, a phenotypic response to a given set of environmental conditions? If this were true, its recurrence would be a matter of no great interest. It seems not to be true for the following reasons:

a) Geographic and temporal distribution of paedomorphic forms is consistent with their constitution as taxonomically-significant biological populations.

i) As would be expected under current notions of geographic speciation, the origin of a paedomorphic offshoot invariably occurs at the periphery of the known range of its parental form (Mayr, 1963; Chapter 16). This is least well documented for *P. b. fasolti*, since the geographic range of Shore Hills populations is so small. Still, this paedomorph is found at the northern extent of the known species range and is more widely separated from its nearest conspecific neighbor than are any other two collections of this age. *P. b. siegmundi* arose at the extreme northwest extent of western *P. b. zonatus; P. b. sieglindae* at the southwest corner of the range of eastern non-paedomorphs. *P. b. bermudensis* had its origin at the northeast periphery of the known range of eastern *P. b. zonatus*.

ii) During the entire St. George's-Southampton interval, *P. b. bermudensis* evolved in isolation on what is now St. George's Island. For a period of up to 120,000 years, paedomorphs and non-paedomorphs occupied non-overlapping geographic ranges in which environmental conditions could not have differed widely.

b) Many living populations of *P. b. bermudensis* have re-acquired features characteristic of ancestral *P. b. zonatus*. In particular, the shell has become thicker and relatively higher (through an increase of the initial form index with no significant modification of the differential growth ratio), and color is intensified so that all three bands have usually formed by the fifth whorl.[1] However, some of the morphological consequences that invariably follow such trends in *P. b. zonatus* do not ensue. A thickened shell invariably produces a stronger callus in *P. b. zonatus;* no callus forms in *P. b. bermudensis*. More important, a recognizable percentage of shells in *all* post-Shore Hills samples of eastern *P. b. zonatus* display the color variation "faded."

[1] Figure 17 does not distinguish modern *P. b. bermudensis* from other post-Shore Hills paedomorphs, but high projections on the fourth axis differentiate the modern samples from all older forms (Fig. 18). In a plot of axis 1 vs. axis 2 of a 4-axis solution, modern *P. b. bermudensis* samples lie midway between the clusters of all post-Shore Hills paedomorphs and *P. b. zonatus* (Fig. 19).

(Pl. 5, fig. 5). This variation, which appears *after* the flame-band transition (usually during development of the fifth whorl), is necessarily absent from paedomorphs that are still in the flame stage at maximal sizes. *P. b. bermudensis* exhibited this weakened coloration during the entire St. George's-Southampton interval; modern *P. b. bermudensis*, which have re-acquired coloration equal in strength to typical *P. b. zonatus*, never display the "faded" variation. I assume that genetic determinants of the callus and "faded" variation were lost from the *P. b. bermudensis* gene pool during the lengthy period in which shells never reached a developmental stage sufficiently advanced for their phenotypic manifestation. In addition to the implication that there exist genetic differences between paedomorphs and non-paedomorphs, this example helps to answer another question: If non-paedomorphs gave rise to paedomorphs four times, why is the reverse transition unknown? Paedomorphosis is a one-way street. Non-paedomorphs must, by definition, possess the capacity for production of the paedomorphic phenotype, for it already exists as an early ontogenetic stage. Paedomorphic populations, on the other hand, will tend to lose genes for features of late ontogeny which can never be brought to phenotypic expression.

Since the four paedomorphic offshoots occupy geographic subdivisions of the species range and differ genetically from the parental stock, separate taxonomic status is warranted. Although defensible on purely morphological grounds, the erection of a single subspecies for the paedomorphs is inadmissible. A form genus is pardonable (since that category is not "real"), but a form subspecies violates population concepts. Therefore, each paedomorphic offshoot has been given separate subspecific status. A visual reconstruction of the evolutionary history of *P. bermudensis* is presented in Figure 20; two of a set of data portrayals according to this scheme constitute Figures 21–22.

D) Cause of Paedomorphosis

1. *Efficient cause.* Rothschild and Rothschild (1939) showed that pulmonates whose gonads had been partly or completely destroyed by parasitic trematodes tended to grow faster and attain larger maximal sizes. Growth curves of many pulmonates display a sharp nick at the point of gonad maturation, indicating a rapid decrease in the growth rate (Boettger, 1952: 469). This rapid slowing of the juvenile growth rate is often accompanied by the development of morphological features that characterize adult forms. Parasitically castrated individuals of *Helix pomatia*, *Arianta arbustorum*, and *Bradybaena fruticum* do not develop typical features of the adult aperture—thickening, coloration, and change in direction of growth (Boettger, 1952). The prolongation of rapid juvenile growth rates may therefore delay the formation of adult characters and produce paedomorphic effects.

If maturation in paedomorphic *P. bermudensis* subspecies occurred at the same number of days after hatching as in non-paedomorphs but at a larger size (due to slower pre-maturational diminution of initially rapid growth rates), then the intensity of gradual allometric alterations that produce typical form differences between juveniles and adults might be correspondingly diminished. Juvenile rates of development would persist longer (in terms of size, though not of time), and such a form, when compared with a typical specimen at a corresponding size near maximum size, would be paedomorphic. The same morphological effect would arise from an absolute delay of maturation in paedomorphs (in time after hatching relative to non-paedomorphs). Thus, paedomorphs either grow faster and mature at the same time as non-paedomorphs, or mature later and thereby prolong the same juvenile growth rate to larger sizes.

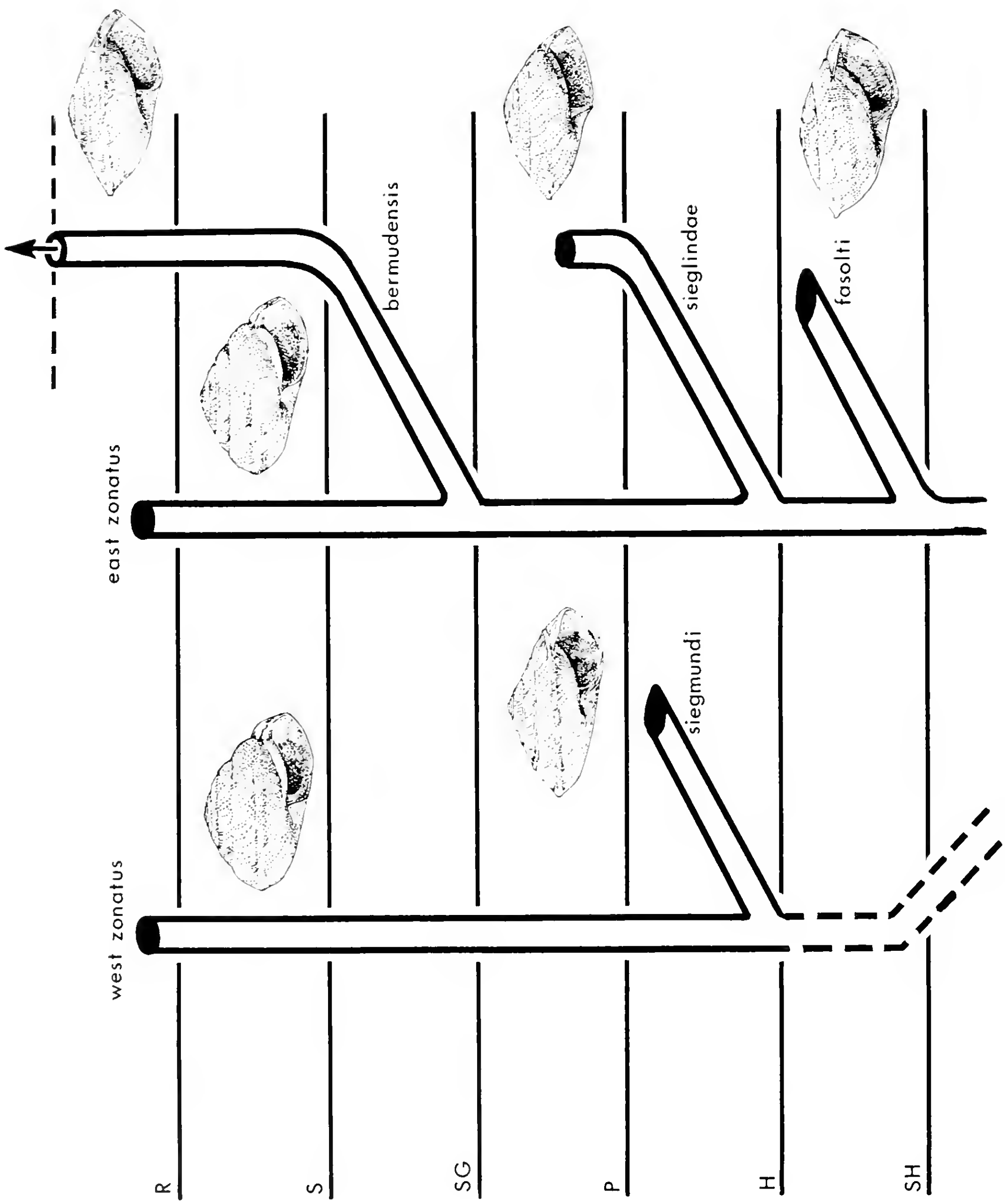

Figure 20. Reconstruction of the phyletic history of *P. bermudensis* showing iterative development of paedomorphic subspecies. SH = Shore Hills; H = Harrington; P = Pembroke; SG = St. George's; S = Southampton; R = Recent.

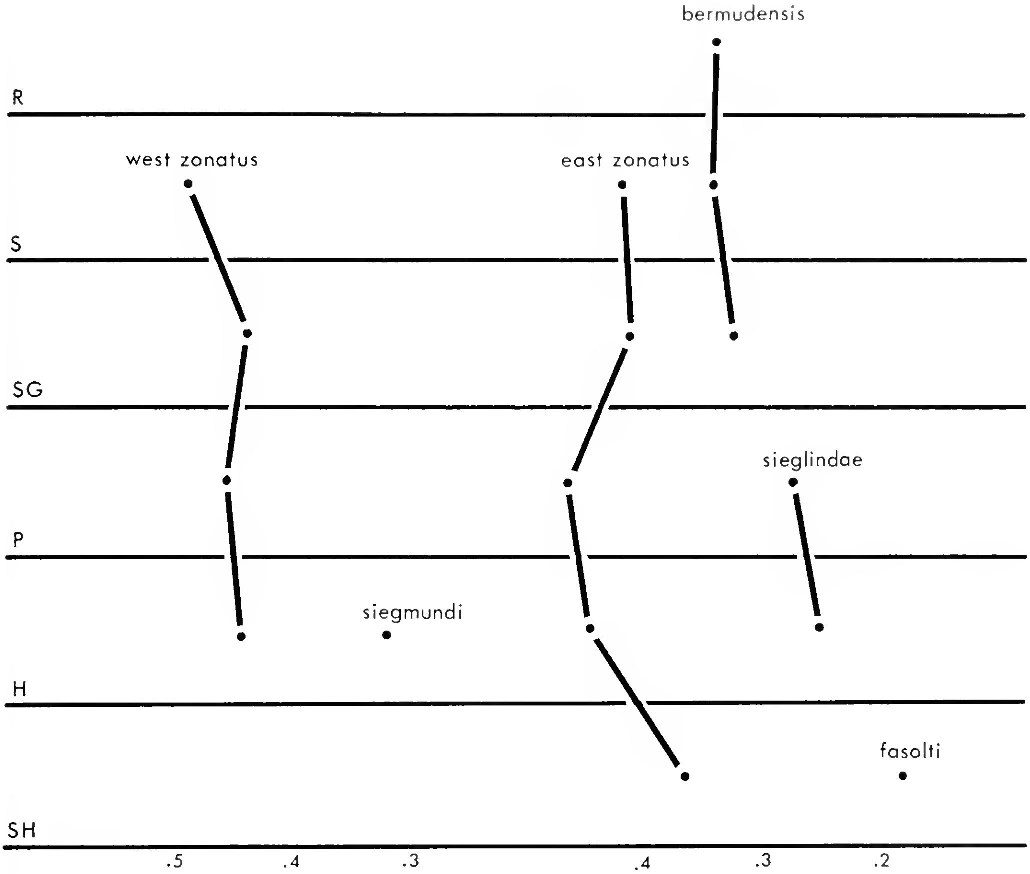

Figure 21. Values for lower eccentricity in *P. bermudensis* displayed in phylogenetic framework. Cited figures are means of mean sample values. SH = Shore Hills; H = Harrington; P = Pembroke; SG = St. George's; S = Southampton; R = Recent.

The weakness of coloration in large paedomorphic shells of *P. bermudensis* can be interpreted in two ways: flames (rather than a band) are produced either because pigmentation is more limited or because a rapid growth rate "spreads thinner" a quantity of pigmentation whose deposition rate is constant per unit of time. Comfort (1951) indicates that this second explanation often applies to pulmonates: "The intensity of pigmentation varies with the growth rate, periods of diapause giving rise very often to darker varices, and periods of rapid growth to paler zones." Likewise, thickness of the callus seems to increase during growth pauses; a sufficiently rapid general growth rate might prevent its formation altogether and, as a further consequence, produce the relatively thin shell characteristic of paedomorphs. I suggest, therefore, that a prolongation of rapid juvenile growth rate (and, by implication, juvenile patterns of ontogenetic allometry) to later sizes is responsible for paedomorphosis in *P. bermudensis*. Since the paedomorphic subspecies reach the same maximal size and whorl number as non-paedomorphs, features which form

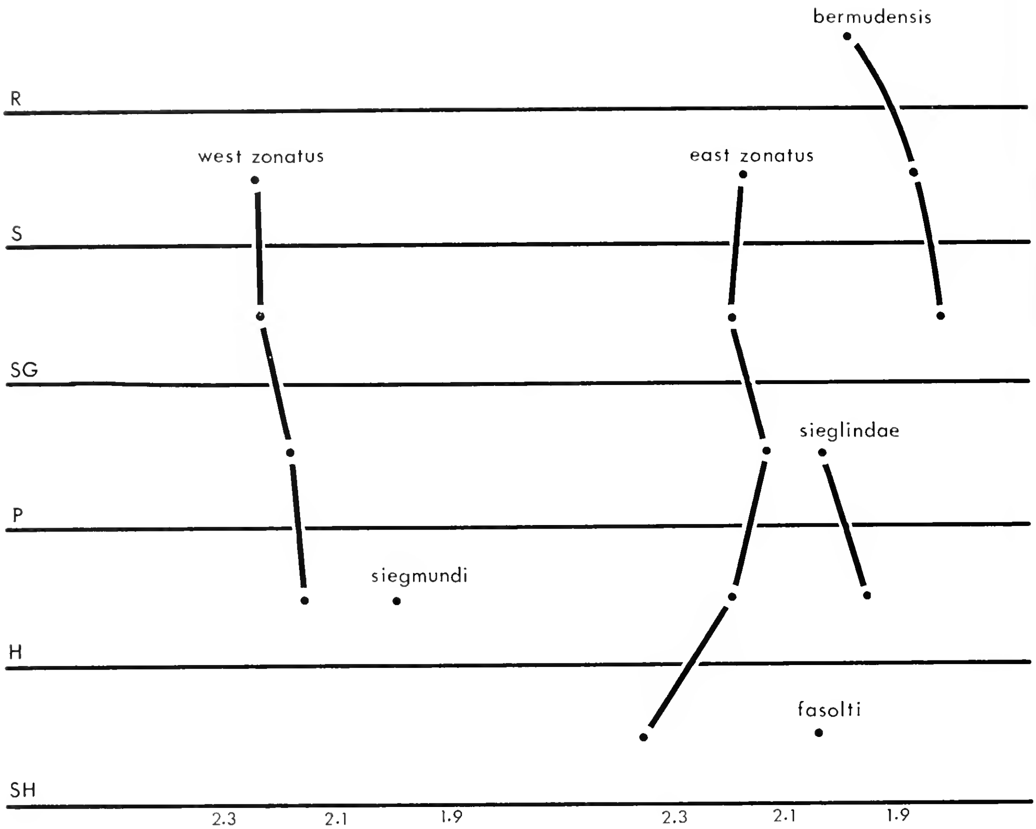

Figure 22. Values for differential growth ratio in *P. bermudensis* displayed in phylogenetic framework. Cited figures are means of mean sample values. Formational symbols as in Figure 21.

during the fourth and fifth whorl of non-paedomorphs are so delayed in appearance that they never form in paedomorphs.

2. *Adaptive significance.* There is an interesting correlation between the incidence of paedomorphosis and depositional environment:

a) Paedomorphosis is most advanced in subspecies originating in red soils. *P. b. fasolti* and *P. b. bermudensis* never possess a callus and rarely (with the exception of some living *P. b. bermudensis*) develop band 1 or 2.

b) Paedomorphosis is less pronounced in subspecies originating in unindurated zones. Bands 1 and 2 are slightly delayed but usually form in *P. b. siegmundi* and *P. b. sieglindae;* a callus is weakly developed in both subspecies.

c) Paedomorphs never originate in eolianites. (*P. b. bermudensis*, living in isolation, survived the period of Southampton dune building, but its geographic separation from competition renders an assessment of its relative adaptability to such an environment impossible).

Red soil conditions seem to favor paedomorphosis; moreover, as will be discussed in the next chapter, both *P. bermudensis zonatus* and *P. nelsoni* tend to have thinner shells in Shore Hills and St. George's times. This may suggest that paedomorphosis served as one pathway to the attainment of a thinner shell, which would have been

adaptive in the limited calcium environment of red soils (Oldham, 1934; Lozek, 1962). That paedomorphosis is not an unreasonably indirect or difficult pathway to such an adaptation is indicated by an R-mode factor analysis of the matrix of means for all *P. bermudensis zonatus* samples. Since non-standardized variables are considered at a uniform size (height + width = 30 mm), the matrix to be factored is analagous to a partial correlation matrix of inter-sample variability with the effect of size removed. The axis 2 grouping of a 7-axis solution includes: aperture width/aperture height and width at fifth whorl/height at fifth whorl projecting positively, and callus thickness, aperture height, and lower eccentricity projecting negatively. Even among non-paedomorphs, a relatively wide shell is associated with a weak callus and a low value of the lower eccentricity. General developmental accelerations and retardations seem to occur within the *P. bermudensis zonatus* stock, whose pattern of intersample variation therefore suggests the latent potential for paedomorphosis—a more pronounced developmental retardation.

IX. PHYLETIC EVOLUTION OF *P. BERMUDENSIS ZONATUS*

A) *Climate and Evolution in Land Snails*

Glacially-controlled oscillation of climate and sea level is the independent variable of Bermuda's Pleistocene history. Neither stratigraphy nor paleontology can proceed much beyond the descriptive without reference to its effects. The cyclothem of Bermudian geology—glacial red soil (solutional unconformity) → interglacial carbonate (eolianite and marine limestone)—is an expression of this oscillation. The temporal recurrence of similar environments leads us to ask whether the morphology of fossils also records the alternating selective pressures of a fluctuating climate. Parallel oscillation of climate and morphology has been recorded in several studies of Pleistocene evolution (in Kurtén's work on fluctuating size trends in fossil bears and, in particular, the changes in coiling-direction frequencies in planktonic Foraminifera—see e.g. Jenkins, 1967).

The relationship of morphology and environment, central to any evolutionary theory, was a subject of intense debate during the late 19th century—a discussion in which land snails figured prominently. J. T. Gulick (1873, 1905) disputed the Darwinian view that geographic variation in the morphology of a species should be referable to selective pressures exerted by environmental differences. From studies on the distribution of *Achatinella* in Hawaii, he concluded that morphological differences arise in identical environments and that geographic separation is a sufficient cause and not merely a precondition of speciation. "The evolution of many different species may take place without any difference in the food, climate, or enemies that surround them . . . Separation without a difference of external circumstances is a condition sufficient to ensure variation" (Gulick, 1873: 504–505).

In defense of the selectionist thesis that he had co-authored, Wallace (1899: 148) replied:

> It is an error to assume that what seem to us identical conditions are really identical to such small and delicate organisms as these land molluscs, of whose needs and difficulties at each successive stage of their existence, from the freshly-laid egg up to the adult animal, we are so profoundly ignorant. The exact proportions of the various species of plants, the numbers of each kind of insect or of bird, the peculiarities of more or less exposure to sunshine or to wind at certain critical epochs, and other slight differences which to us are absolutely immaterial and unrecognizable, may be of the highest significance to these humble creatures, and be quite sufficient to require some slight adjustments of size, form, or colour, which natural selection will bring about.

This debate extended beyond snails and beyond the role of selection in evolution, for basic intellectual attitudes were involved. As originally formulated, the

Darwinian approach was highly deterministic in accord with prevailing notions of the nature of natural science. To invoke the term "science" was to imply a deterministic model—witness the "scientific socialism" of Marx and its theory of ineluctable historical progression. This attitude is quite explicit in Wallace's rebuttal of Gulick:

> If the average characters of the species are the expression of its *exact adaptation* to its whole environment, then, given a precisely similar environment, and the isolated portion will *inevitably* be brought back to the same average of characters (Wallace, 1889: 149; my emphases).

Rev. Gulick was a participant in the late 19th century antimechanist reaction which, in another guise, culminated in vitalism and the "creative evolution" of Henri Bergson:

> If my contention [that different species of a genus can arise in identical environments] is in accord with the facts, the assumption which we often meet that change in the organism is controlled in all its details by change in the environment, and that, therefore, human progress is ruled by an external fate, is certainly contrary to fact (Gulick, 1905: iv).

Our contemporary reconciliation, which has affirmed and extended the role of selection within the non-mechanist framework of modern evolutionary theory, has incorporated much of Gulick's attitude and some of his empirical conclusions (e.g., the emphasis on geographic isolation in speciation).

Amidst the excitement provoked by rediscovery of Mendel's work, Crampton (1916) again focused on the relationship of environment and morphology in his study of *Partula*. The "causal value of the 'environment' in producing varietal modifications" was, to Crampton (1916: 48), the "major problem." He concluded:

a) "The originative influence of the environment seems to be little or nothing" (1916: 12).

b) "The morphological differences observed are due to spontaneous congenital causes that remain unknown in themselves, but whose effects are produced quite independently of the external conditions" (1916: 48).

Darwin had answered only one of the two great questions; he had explained the production of new forms by natural selection of variants but had not discovered the source of variation—and this "Origin of the Fittest" (as Cope entitled his book) was to many evolutionists the more important issue. The early mutationists thought they had found the key to this origin in Mendel's laws (second quote above) and relegated natural selection to the non-creative function of headsman:

> The role of the environment is to set the limits to the habitable areas or to bring about the elimination of individuals whose qualities are otherwise determined—that is, by congenital factors (Crampton, 1916: 311).

Both neo-Lamarckians and early mutationists denied selection a creative role, the former because variation was inherently directed towards adaptation, the latter because adaptations arose in a single step. The truly creative function of selection, continual and successive preservation of the adaptive component from a random spectrum of variation, was perceived by neither. Crampton remarked: "Some among the neo-Darwinians endeavored to make natural selection originative as well as discriminatory, but their views have not gained wide acceptance" (1932: 187).

It is ironic that Crampton, in his efforts to discredit neo-Larmarckism by denying to the environment an "originative influence," joined Cope and Osborn in failing to grasp the importance of selection. To deny direct environmental induction is not, of course, to eliminate the possibility that morphology and environment are related, for the role of environment is to determine the direction of selection.

In the initial stages of its development, a new theory is often taken by its proponents as all-encompassing; only later are syntheses effected with the cogent aspects of earlier views. In assigning to mutation

TABLE 12. CORRELATION OF MORPHOLOGY AND CLIMATE IN *P. BERMUDENSIS ZONATUS*: FLUCTUATING TRENDS IN WHORL SIZE AND SHELL THICKNESS. Total number of specimens and number of samples shown under column headed N; the means and ranges cited in the table are compiled from mean sample values. In the tabulation of ranges, the value of the anomalous Spittal Pond St. George's sample is recorded separately, but included in the calculation of the mean. For this sample, size at the fifth whorl is 16.35 mm; callus thickness is 0.177 mm. All measures in mm.

	N	Size at Fifth Whorl	Callus Thickness
Southampton	62 (4)	16.28 (15.74–16.77)	0.383 (0.236–0.551)
St. George's	65 (5)	14.93 (14.47–14.67)	0.138 (0.010–0.229)
Pembroke	68 (4)	16.00 (15.71–16.41)	0.233 (0.193–0.295)
Harrington	95 (5)	15.45 (15.30–15.82)	0.279 (0.259–0.341)
Shore Hills	76 (4)	13.42 (12.85–13.99)	0.180 (0.141–0.223)

("spontaneous congenital factors") the role of both material *and* efficient cause of evolutionary change (instead of just the former as agreed today), Crampton failed to appreciate the indirect influence of environment in producing evolutionary change.

With the infusion of population concepts into evolutionary thought, the adaptive nature of geographic variation in land snails has become accepted. Welch (1938, 1942, 1958) studied the Hawaiian *Achatinella* anew and in far greater detail than Gulick had done. He found definite correlations of form and size with altitude, moisture, and temperature among subspecies of *Achatinella mustelina* (Welch, 1938). Bailey (1956) attributed some of Crampton's "non-adaptive" variation to the results of selection. Studies were made of the phenotypic effects of different environments upon land snail shells (Oldham, 1934; Rensch, 1932) and results were used to interpret genetically determined variation in adaptive terms (Rensch, 1937). Work on *Cepaea* demonstrated that the distribution of color variation corresponds well with inferred environmental selective pressures (review in Harvey, 1964; Ford, 1964).

While so much excellent work on the adaptive nature of infraspecific geographic variation has been produced, virtually nothing is known of the nature of temporal variation within pulmonate species. Pulmonate paleontologists have confined their climatic concerns to species distribution patterns and have not studied morphological variation within a species living through a temporal succession of environments (reviews in Lozek, 1965; Taylor, 1965; and la Rocque, 1966). Temporal variation in *P. bermudensis zonatus* will be considered in this chapter.

B) Correlation of Environment and Morphology

Unlike that of *P. nelsoni*, the morphology of *P. bermudensis zonatus* exhibits no immediately recognizable correlation with lithology and, by implication, climate. However, a highly significant pattern can be inferred from the measurements. This pattern parallels noted trends of the *P. nelsoni* stock and proves that glacial and interglacial climates are associated with characteristic morphologies in four lines (*P. nelsoni*, *P. superior*, eastern and western *P. bermudensis zonatus*).

a) shell thickness: Strength of the parietal callus is a good measure of relative shell weight. In Shore Hills (glacial) times, the callus of *P. bermudensis zonatus* was weakly developed at the standard size. Shell thickness increased during the succeeding interglacial (Harrington-Pembroke) only to fall again to Shore Hills levels with the return of glacial climates during the St. George's. The double oscillation was completed when Southampton (interglacial) snails reacquired strong calluses (Table 12, Fig. 23).

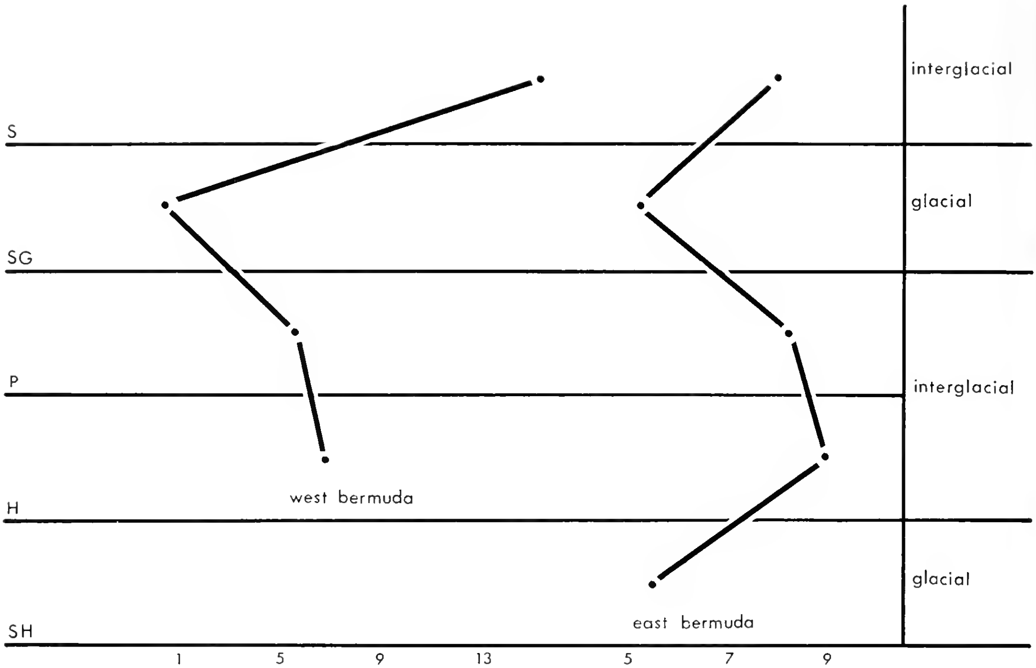

Figure 23. Correlation of shell thickness (callus) and climate in western (left) and eastern stocks of *P. bermudensis zonatus*. SH = Shore Hills; H = Harrington; P = Pembroke; SG = St. George's; S = Southampton.

b) shell size:

i) maximum size: With a range of maximal shell size far smaller than that of *P. nelsoni* or *P. cupula*, little can be done with this variable in *P. bermudensis* due to great differences in sample size. I can state with fair certainty only that the largest Shore Hills snails surpass those of all more recent populations in maximal size. For more recent forms, I compiled means for the five largest specimens in each sample. The only consistent result of this procedure is the artifact that larger samples tend to have larger mean values. Grand means for each post-Shore Hills formation are: Harrington, 34.3 mm; Pembroke, 34.4; St. George's, 34.2; Southampton, 33.5. The largest St. George's sample (Spittal Pond, locality 32) has fewer specimens than *any* of the measured interglacial samples. If the sample-size artifact controls values of the grand means, then an unbiased sampling procedure might predict that St. George's specimens tend to be somewhat larger in maximal size.

ii) standardized size-at-fifth-whorl: Parallel oscillation of size-at-fifth-whorl and lithology is pronounced and consistent (Table 12, Fig. 24). Values of this measure are low in red soils, intermediate in unindurated zones (Harrington) and high in eolianites (Pembroke, Southampton). In three localities, Harrington and Pembroke snails were found in continuous sequence, inches apart in direct superposition—a strong indication that genetic continuity was maintained during the lithologic transition. In all cases (*P. b. zonatus* from Whalebone Bay, locality 1, and Town Cut, locality 87, and *P. b. sieglindae* from Rocky Bay, locality 44), Pembroke samples exhibit larger mean sample values of size at fifth whorl (significant at 5 per cent level in all

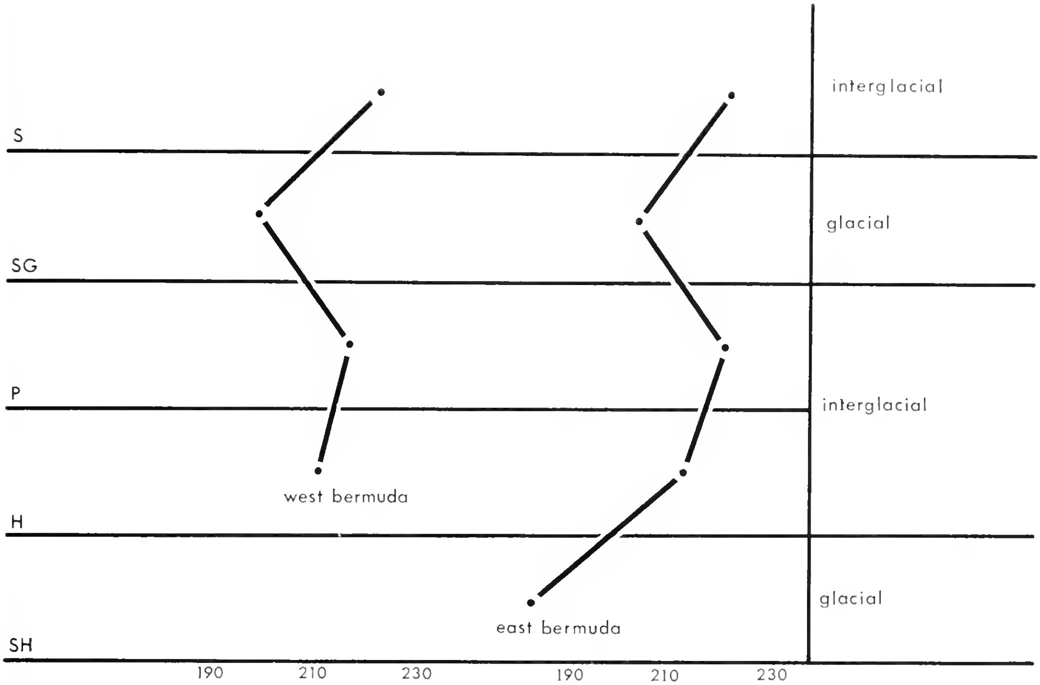

Figure 24. Correlation of size at fifth whorl and climate in western (left) and eastern stacks of *P. bermudensis zonatus*. Formational names as in Figure 23.

eases). The consistency of this correlation is even stronger than that for callus thickness. Leaving aside the St. George's Spittal Pond sample which is anomalous in all respects, the largest mean size-at-fifth-whorl for a red soil sample (14.67 mm, St. George's at Saucos Hill, locality 41) is a good deal less than the smallest eolianite value (15.30 mm, Harrington at Whalebone Bay, locality 1).

In conclusion, snails from red soils (glacial periods) tend to reach larger maximal sizes, have thinner shells and be smaller at a whorl than samples from eolianites.[1]

In *P. nelsoni*, apparent temporal fluctuations in morphology were interpreted as artifacts of an imperfect record. Two subspecies lived side by side from Shore Hills to St. George's and their alternating superposition in a single section reflects the migration of their preferred environments. I favor the literal interpretation of zig-zag evolution (Henningsmoen, 1964) for fluctuating trends in *P. b. zonatus* for the following reasons: The differences between red soil and eolianite *P. nelsoni* and *P. superior* are large and numerous (involving color—usually considered a better indicator of taxonomic distinction than form—as well as shape). The correspond-

[1] As in *P. nelsoni*, small size at a whorl can be an artifact of small protoconch size, but this is not true here. Average protoconch widths for *P. b. zonatus* samples of all formations are remarkably similar. In another case, the decrease in whorl size of modern *P. b. bermudensis* compared with St. George's and Southampton forms, the artifact may be involved since living populations tend to have small protoconchs. Phyletic size decrease in *P. b. bermudensis* may be related to increased competition and decreased food resources caused by the recently introduced fauna (both human and pulmonate).

ing differences in *P. b. zonatus* are few and small, involving only those features which adapt the snail to its new environment (see next section) and only those magnitudes small enough to be encompassed by the phenotypic plasticity of a subspecies. I prefer the zig-zag hypothesis not because it is "simpler" *per se*[1] but because I would be surprised if the genetic determination of shell form is so precise that a local population cannot decrease the shell thickness of its members, but must give way to another already possessing the requisite thickness whenever such a modification is required by the conditions of life.

These single variable results are individual cases of a more general coherence. I had thought that quantitative appraisal of samples of this relatively conservative stock in a short time sequence might produce a haphazard clustering of samples, but Q-mode plots demonstrate that the samples of each temporal unit tend to associate. This may be due to the uniqueness of complex selective pressures in any given environment[2] or to genetic interchange among contemporaneous samples. The coherence, in any event, is an encouraging datum for the use of multivariate biometry in evolutionary studies.

The uniqueness of Shore Hills samples was demonstrated in Figure 17. To gain a better idea of subgrouping within the post Shore-Hills samples, I eliminated the Shore Hills data and ran another analysis. The numbers of Figures 25 correspond to the following samples: Harrington, 01–05; Pembroke, 06–09; St. George's, 10–13; Southampton, 14–17. As in *P. cupula* plots of Chapter 6, relative width of band 3 is the only color variable included; hence, distinction between eastern and western snails is not effected.

The St. George's red soil snails sort separately from eolianite samples. Within the eolianite cluster, Harrington samples (from an unindurated zone) are associated at the periphery of the cluster, closest to St. George's specimens. Samples from Pembroke and Southampton dunes are furthest removed from the St. George's snails. Only the anomalous Spittal Pond St. George's collection (number 13 — unintentionally) disrupts the general trend by grouping with the Pembroke snails.

C) Adaptive Significance of Oscillating Trends in Morphology

To learn the significance of this correspondence between morphology and lithology, we must discover what environments these lithologies imply and see how modern pulmonates vary in such habitats. Red soils were deposited on Bermuda during periods of continental glaciation; dune building occurred in interglacial environments (Bretz, 1960; Land, Mackenzie, and Gould, 1967). At a minimum, the environment of pulmonates living in red soils was, in comparison with that of eolianites,

a) colder

b) wetter (Bryan and Cady, 1934; J. Chase and A. MacIntyre, personal communication)

c) poorer in available calcium for shell building. Bermudian dunes are composed of calcareous organic fragments. The

[1] Ockham formulated his razor to wield against the Platonic notion that universals existed in the real world. These universals were the entities that had been multiplied beyond necessity, and they were unnecessary precisely because they were inventions of the intellect. Thus, the razor, as used by Ockham and the early nominalists, was not a device to distinguish the better of two empirical postulates, but a method to simplify logic by the elimination of unnecessary non-empirical attributes. It is a shame that the razor is so often invoked improperly by modern scientists. We can all think of cases in which the more complex of two consistent empirical hypotheses provided a more satisfactory interpretation of a phenomenon. I do not deny that simpler explanations usually turn out to be more acceptable, but merely point out that the razor should not be cited as a *deus ex machina* to prove the case.

[2] Many simple selective pressures recur with similar basic environments, but the entire complex of pressures will not be exactly duplicated, if only because no two environments can ever be precisely alike.

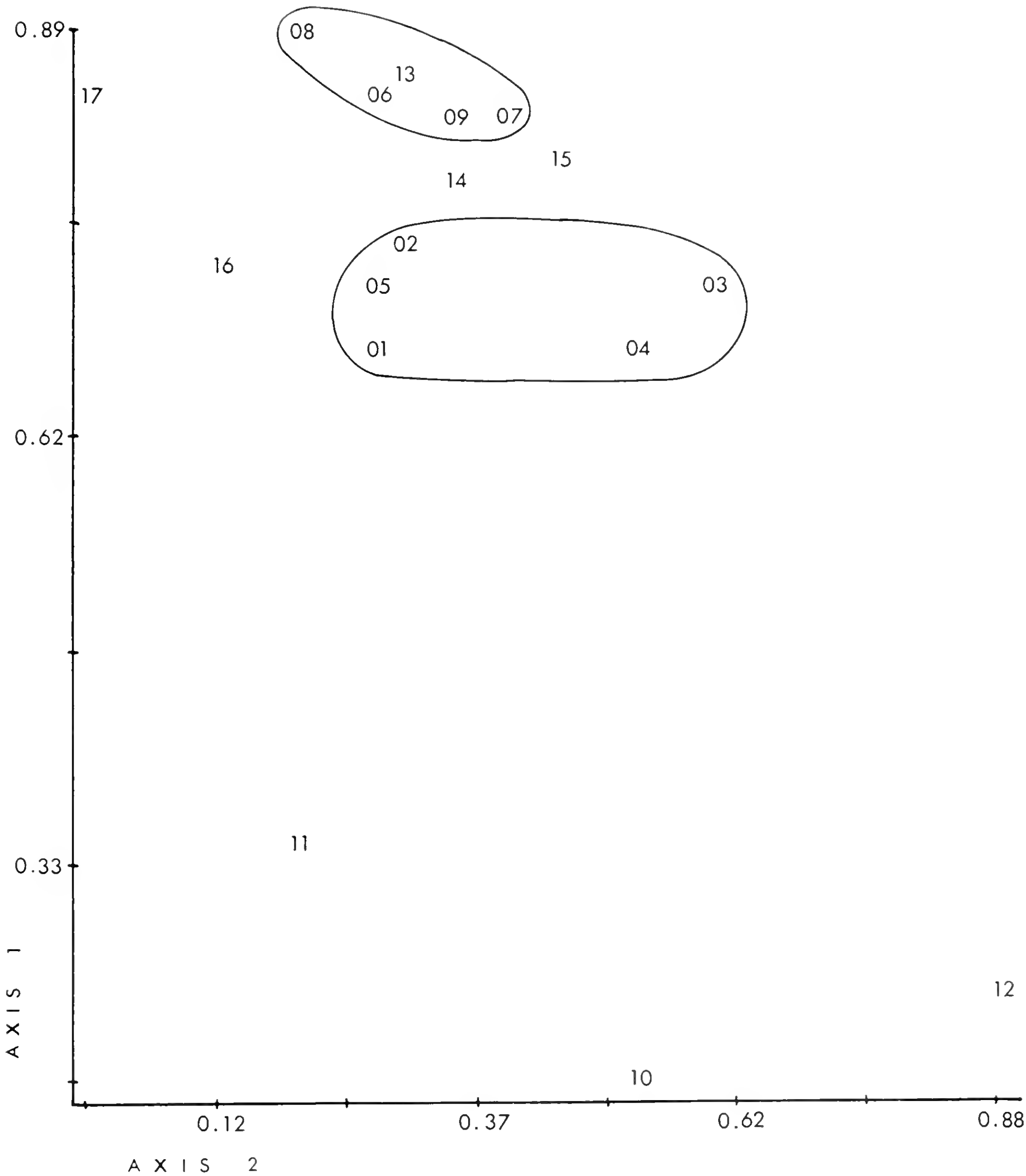

Figure 25. Plot on varimax axes for all post-Shore Hills *P. bermudensis zonatus* (minus Ireland Island St. George's, for which only 5 specimens were available). Upper circle includes all Pembroke samples and the anomalous Spittal Pond St. George's. Lower circle includes all Harrington samples. Normal St. George's at bottom.

$CaCO_3$ content of eolianites and unindurated zones ranges from 92.6 to 99.3 per cent (Ruhe *et al.*, 1961). Sayles (1931) determined the CaO content of a deep red phase and "pink variant" of the St. George's soil as 3.13 and 50.31 per cent, respectively. Ruhe *et al.* (1961) obtained values as low as 1.9 per cent for the $CaCO_3$ content of red soils.

The effect of these factors on pulmonate shells has provoked some interest and a widely scattered literature:

a) effect of temperature:

i) on maximal size: Likhachev and Rammel'meier (1952: 27) note that northern land molluscs of the USSR tend to be small. McGuire (1966), on the other hand, has stressed the adaptive advantages of large size at low temperatures. Most pulmonate workers are agreed that each form tends to have a temperature optimum above or below which maximum size decreases. Rensch (1932) found that several European species were characteristically smaller in regions of higher annual temperature. Since we cannot know the optima of extinct taxa, the effects of temperature cannot be inferred.[1]

ii) on shell thickness: J. W. Taylor (1900) and Likhachev and Rammel'meier (1952) noted a relationship between colder temperatures and thin shells, but Rensch (1932) could find no correlation between relative shell weight and temperature in his study of several European genera.

b) effect of precipitation:

i) on maximal size: Rensch (1932: 758) cites a large number of studies which indicate that local populations living in drier climates tend to reach smaller adult sizes than those of the same species in wetter regions. Geyer (1927, quoted in Rensch, 1932: 778) proposed that longer feeding periods between diapauses in areas of high rainfall tended to produce larger and thinner shells.

ii) on shell thickness: Geyer's conclusion has already been cited. Of all correlations between morphology and environment, Rensch (1932) found the strongest to be that of increased shell thickness with augmented solar illumination of dry climates.

c) effect of calcium availability:

Many authors have stressed the correlation of pulmonate distribution patterns with the presence of limestone outcrops. In calcium-poor areas of Czechoslovakia, Lozek (1962) has found snails crowded on the ruins of medieval castles and churches where disintegrating mortar furnishes a source of lime. Talmadge (1967) correlated the abundance of coastal land snails with the distribution of lime in drift shells, guano, subfossil marine shells, and Indian middens. On acidic islands off Nova Scotia, *Cepaea hortensis* obtains its lime from shells dropped by gulls (Bleakney, 1966). Many pulmonates are dependent upon direct ingestion of limestone for the construction of their shells. *Murella murella sicana* bores holes in limestone and incorporates the ingested material (which may comprise more than 90 per cent of the gut contents) into its shell (Rensch, 1932: 791–793). Rensch (1932) grew *Murella murella globularis* in a calcium-free environment; the shells produced were paper thin and the animals died before they were half grown. Snails so deprived of calcium will often eat empty shells (Rensch, 1932: 790; Smith, 1966: 248).

Oldham investigated the relationship between calcium availability and shell thickness for several genera (1929, 1934). In one experiment, young *Helix aspersa* of the same size were divided into two groups, one fed on cabbage, oatmeal, and chalk, the other on cabbage and oatmeal alone. One year later, the shells were approximately the same size, but those of animals whose diet included chalk were 4.5 times

[1] Unfortunately, the size at a whorl criterion has never been used in environmental studies of recent pulmonates. Work has been virtually confined to helicids and other groups with definite adult sizes. Adult size alone has been studied in relation to climatic factors.

as heavy. Other references to the positive correlation of shell thickness with calcium availability include Boycott (1934), Robertson (1941), Schmidt (1955), and Frank and Meyling (1966).

An impressive array of independent phyletic events in *P.* (*Poecilozonites*) points to the conclusion that calcium availability is the controlling factor of shell and callus thickness:

1. *P. nelsoni:* a thin-shelled subspecies lived in red soils; the eolianite subspecies has a thick shell and strong callus.
2. *P. superior:* the shell is thin in *P. s. superior* from the Shore Hills red soil and thick in *P. s. arenicolus* from Harrington-Pembroke eolianites.
3. Shell and callus thickened in the transition from Shore Hills to Harrington and again in the passage from St. George's soil to Southampton eolianite in both eastern and western stocks of *P. bermudensis zonatus* (up to four independent events).
4. The most paedomorphic, and therefore the thinnest shelled, subspecies of *P. bermudensis* evolved in red soils (*P. b. fasolti* and *P. b. bermudensis*).
5. The single eolianite sample of red-soil, thin-shelled *P. n. nelsoni* is thick shelled; the single red-soil sample of eolianite, thick-shelled *P. s. arenicolus* is thin shelled.
6. The most vigorous dune development in Bermuda occurred during Southampton times on the southwest portion of the main island. Shell and callus thickness of *P. b. zonatus* from these eolianites (Sand Quarries, locality 73, and Horseshoe Bay, locality 75) exceed that of all other samples.
7. Modern *P. b. bermudensis* living on exposures of the ancient red soils (Biostation, locality 78, and Perfume Factory, locality 82) have thinner shells than those living on weathered eolianite (Church Ruins, locality 79, and Crawl Point, locality 81).

More intriguing perhaps than the sheer volume of reported instances are the "multiple solutions" utilized by different taxa to obtain the required adaptation: two long-ranging subspecies in *P. nelsoni* and *P. superior*, branching of peripheral isolates by paedomorphosis in *P. bermudensis*, and zigzag fluctuations in the central stock of *P. b. zonatus*.

In conclusion, the effects of temperature cannot be determined. Wetter climates might induce larger and thinner shells. Thin shells will be built when the calcium supply is limited. Since the inferred red-soil environment is colder, wetter, and calcium-poor, the larger size and thinner shells of its snails conform to the expected correlations. The major temporal variations of morphology in the *P. b. zonatus* stock are adaptive in nature.

Oscillating trends in morphology correspond to selective pressures of fluctuating environments, but this observation does not permit an answer to what Mayr and Rosen called "the first question" in their work on geographic variation in *Cerion:* "The first question is to what extent the differences between populations have a genetic basis, or reciprocally to what extent the phenotype of a colony is modified by the effects of the local environment" (Mayr and Rosen, 1956: 42). Limited supplies of calcium evoke selective pressures favoring genetic combinations that produce thin shells, but, as Oldham (1929, 1934) showed, thin shells may also be a simple phenotypic response to lack of building materials; the same adaptive feature may be produced by either route. When morphology alone is available as evidence, it may be impossible to infer the genetic basis of infraspecific variation.

Several guides often employed by paleontologists to distinguish genetic from non-genetic variation are fallacious. McGuire (1966: 895) writes of "nongenetic responses or reversible adaptations to local conditions," but phenotypic results of genetic responses involving general measures of size and shape are readily reversible (Dollo's law, a consequence of probability theory, increases in applicability as structures become complex—

Gould, in press). The absence of definable trends has been taken as an indication of non-genetic variability: "Faunas at each level may be morphologically defined, but few consistently maintained evolutionary trends have been observed. Shell form seems particularly subject to independent, and probably phenotypic variation" (House, 1965: 79); but the complexity of selective pressures in intricately fluctuating environments may produce a pattern of genetically-based variation that seems random. The Bermudian environment approaches the simple model of a two-state oscillation; adaptive morphological responses are similarly uncomplicated.

This inability to distinguish genetic from non-genetic variation has been perceived as a major dilemma by students of pulmonates (Welch, 1958, on geographic variation in *Achatinella;* Rensch, 1932, on the albinism of xerophiles). It has bothered many other evolutionists (Best, 1961, on the spacing of axial tubercles in the trilobite *Encrinurus ornatus;* Mitra, 1958, on basic shape ratios in the brachiopod *Goniorhynchia boueti;* Jolicoeur, 1959, on geographic variation in modern North American wolves; and Nichols, 1962, on local populations of the heart urchin *Echinocardium cordatum* in the British Isles). In each of these instances, morphology was found to be well adapted to a geographic pattern of environmental variation. In *P. b. zonatus*, temporal variation of environments elicits an adaptive response, and I am equally unable to assess the contributions of genetic and non-genetic factors to these adaptations. The extent of morphological alteration is not inconsistent with a purely phenotypic response, but the temporal duration of each successive morphological stage might lead to the implication that some genetic modification is involved. Regardless of the basis of the change, however, oscillations of environment elicit adaptive morphological responses (directly or indirectly); the relationship of climate and morphology in the phyletic history of *P. bermudensis zonatus* is affirmed.

X. INTERSPECIFIC HYBRIDIZATION IN *P.* (*POECILOZONITES*)

Carlquist (1966: 263) lists the following among his principles of island evolution:

"Natural hybridization acquires a positive value in evolution of the waif biota."

Cut off from the inflow of new genetic material by oceanic barriers and limited in population size by the area of small islands, extensive interspecific hybridization provides an advantageous mechanism for the dispersion of genetic variability. Maximization of outcrossing is common among plants of waif biotas (Carlquist, 1966).

Interspecific hybridization is fairly common in pulmonates. Cooke (1931) found four hybrid colonies of *Cariella* in boundary zones between species. Lang (1908) described hybrids of *Cepaea nemoralis* and *C. hortensis.* In other cases (Pilsbry, 1912; Mayr and Rosen, 1956), the status of colonies intermediate between two populations is difficult to assess because the taxonomic separation of parental forms has not been adequately ascertained: "The [increased] variability [of intermediate colonies] is either due to true introgression (gene exchange between species) or due to gene flow among well-differentiated allopatric populations of the same species" (Mayr and Rosen, 1956: 1).

Three potential cases of interspecific hybridization, one fairly certain, one probable, and one possible, have been detected between *P. bermudensis* and *P. cupula.*

1. Bus Stop, locality 3: Shore Hills and Harrington snails exposed in a road cut at the first bus stop northwest of Flatts[1] on

[1] This area is topographically above the upper limit of Devonshire seas. Deposition was continuous throughout the Shore Hills-Harrington interval; the inception of Harrington conditions is indicated by an influx of carbonates diluting the deep red Shore Hills to a pink hue.

Table 13. Analysis of variance for variables significant at 5% level among three groups constructed from hybrid bus stop sample

Variable	F Value	Mean of *bermudensis* Like	Mean of Interme-diate	Mean of *cupula* Like
Relative width of band 2 at 4th whorl	83.81	0.845	0.710	0.430
Relative width of band 2 at 5th whorl	46.19	0.841	0.732	0.498
Relative width of band 3 at 5th whorl	26.80	0.318	0.246	0.221
Initial form index	6.49	0.199	0.242	0.216
Total height plus total width	4.75	28.05	28.29	31.12
Length of aperture	4.45	8.24	8.09	9.06
Height of aperture	3.96	6.36	6.55	7.10
Height at 2nd whorl	3.36	0.937	1.075	1.017

the road to St. George's lack a callus as in *P. cupula* but seem, for the most part, intermediate in shape between *P. bermudensis zonatus* and typical *P. cupula cupula*. A complete and even intergradation in banding pattern from the *cupula* $12^{n}3$ type with sharp band margins to the *zonatus* 123 with diffuse margins is found among the shells of this hybrid population (Pl. 5, figs. 1a–1c).

I selected from the sample three groups of 10 specimens, basing discrimination entirely upon the width and marginal definition of bands 1 and 2. *F* tests were performed on each variable for the three groups (most *cupula*-like, most *zonatus*-like, and intermediate); Table 13 presents a chart of all variables in which significant differences were detected at the 5 per cent level among groups.

The probability of among-group differences in color measures exceeds by a thousand fold that of any size or shape measure. This is, of course, primarily an artifact of the criterion used to define groups, but the reality of far greater color variability can be glimpsed by considering the total observed range of values implied by within-group means. Population variability is average for the highly polygenic characters of size and shape and abnormally high for color measures, which, by analogy to studies of banding in modern pulmonates, have a simple genetic basis. Mayr and Rosen (1956) observed a similar phenomenon in hybrid populations of *Cerion*. "Although hybridization does not necessarily lead to an appreciable increase of phenotypic variability, as shown, for instance, in the case of such highly multifactorial characters as size, there will be an increase in variability for characters with an oligogenic basis. This has in fact been shown in all known cases of hybridization" (Mayr, 1963: 131).

Statistically significant differences in three non-standardized variables (final size, length of aperture and height of aperture) have no biological significance. They are artifacts of the circumstance that four of the measurable *cupula*-like specimens were among the absolutely largest shells of the population (several *zonatus*-like specimens which could not be measured due to protoconch injury are even larger). Significant differences in initial form index and height at the second whorl are referable to a common factor. As expected, early whorl heights of *cupula*-like shells exceed those of *zonatus*-like individuals, but the values for intermediate specimens surpass all others. In his study of interspecific hybrids of *Cepaea nemoralis* and *C. hortensis*, Lang (1908) found that while most characters were intermediate with respect to parental forms, average

values for some measures exceeded that of either progenitor.[1]

2. Fort Scaur, locality 69: Abnormally high-spired shells displaying most characteristics of western *P. b. zonatus* are found in a brownish soil of unknown age exposed on the main road at Fort Scaur. (Width/height at fifth whorl = 0.89; lowest for normal *P. b. zonatus* is 1.14. Differential growth ratio and initial form index are 2.44 and .326, respectively, both exceeding any *P. b. zonatus* value.) Although spires of such height are known only in two *P. cupula* subspecies, I would ascribe the Fort Scaur values to convergence were it not for the observation that some specimens of this population exhibit the $02^{n}3$ pattern (Pl. 5, fig. 2), unknown in *P. bermudensis* but found as the most common morph in both high-spired *P. cupula* subspecies (*P. c. dalli* and *P. c. multispira*). (Most Fort Scaur shells have a strong callus and the 023 band pattern.)

3. South Shore local populations of *P. cupula cupula:* These shells, which are "pure" *P. cupula* in the lack of a parietal callus and invariable presence of the $12^{n}3$ band pattern, are unlike typical local populations of *P. cupula cupula* and strikingly similar to *P. bermudensis zonatus* in general measures of size and shape. Although some introgression may be involved, the ascription to convergence of size and shape similarities between these shells and *P. b. zonatus* seems more reasonable, since no color intermediates are known. The most probable case of interspecific hybridization in *Poecilozonites* involves the same local populations and is characterized by complete intergradation of color patterns.

Geographic distribution of the species of *P.* (*Poecilozonites*) is consistent with hypotheses of hybridization. *P. nelsoni* and *P. cupula*, often found in association, never hybridize; *P. cupula* and *P. bermudensis zonatus* had different ecologic preferences, for although their areas of distribution overlap extensively, the two species are never found as such at the same locality. When unusual circumstances brought the two species into direct contact, hybrids seem to have been produced.

In order to assess the relative similarity of proposed hybrids to measured samples of the parental species, a Q-mode factor analysis was performed on the matrix of means of all samples of the two species (Appendix 3). This is a comparison of form alone; all color variables were eliminated, since the identification of hybrids and the discrimination of species is based primarily on color—i.e., we know that color will effect a distinction and wish to discover the diagnostic capacities of a multivariate consideration of form. Numbers 1–36 of Figure 26 represent the same samples (of *P. bermudensis*) as in Figures 17–19 (description in Chapter 8). Numbers 37–57 as follows:

Proposed hybrids:

1) Bus Stop local population: 57
2) Fort Scaur local population: 56
3) South Shore local population of *P. c. cupula:* 37–43

P. cupula:

4) *P. c. cupula:* Gibbet Island local population: 44
5) *P. c. cupula:* Whitby local population 45
6) *P. c. cupula:* Walsingham local population: 46
7) *P. c. triangularis:* Pink Beach Road local population: 47
8) *P. c. triangularis:* Devil's Hole local population: 48
9) *P. c. cupuloides:* Quarry Road local population: 49, 50
10) *P. c. cupuloides:* Coney Island local population: 51
11) *P. c. cupuloides:* Bird's Nest local population: 54

[1] Also relevant to this case is Lang's observation (1908) that the mouth coloring of hybrids was indistinguishable from that of *C. nemoralis*. Absence of a parietal callus (a *P. cupula* feature) in all Bus Stop shells is consistent with the interpretation that they are hybrids.

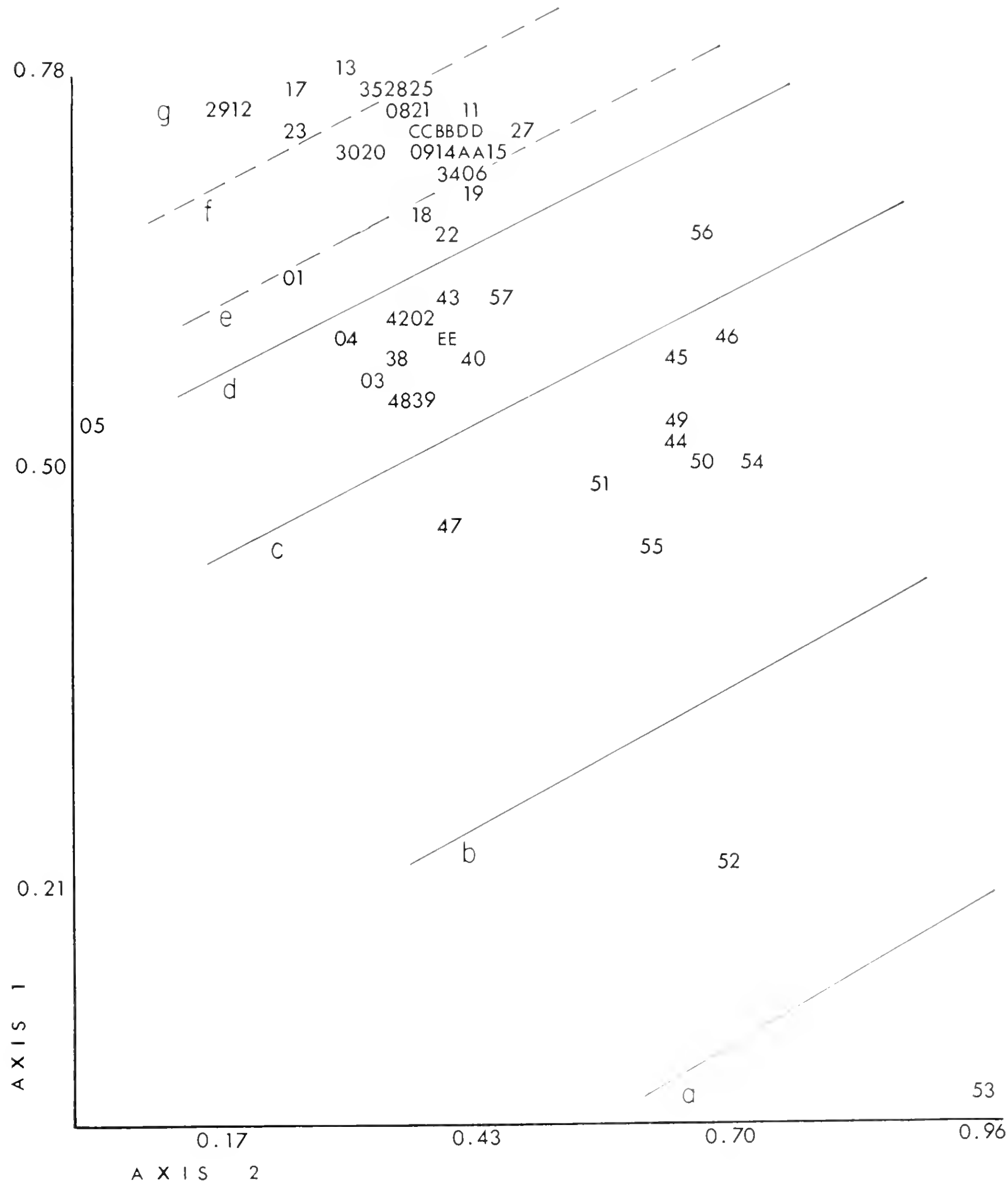

Figure 26. Plot on varimax axes for all measured samples of *P. cupula* and *P. bermudensis* (see text for explanation). AA stands for 07 and 10, BB for 16, 24, and 36. CC for 31 and 32, DD for 26 and 33, EE for 37 and 41.

12) *P. c. cupuloides:* Surf Bay local population: 55
13) *P. c. multispira:* St. David's Island local population: 52
14) *P. c. dalli:* Albuoy's Point local population: 53.

Sample projections on the first and second axes of a 5-axis solution assume a fairly strong upper left to lower right orientation (Fig. 26), in which several clusters are clearly delineated. (The basically linear orientation is better seen in a 2-axis solution, which still accounts for 95.7 per cent of the total information.) At the lower extreme of the distribution are found the smallest[1] and highest-spired forms (*P. c. dalli* and *P. c. multispira*); at the upper extreme, the largest and lowest-spired (the paedomorphs *P. b. siegmundi*, *P. b. sieglindae*, and *P. b. bermudensis*). When the array is separated into components by construction of lines normal to the trend, the following groups are defined (from lower right to upper left; solid lines separate clusters, dotted lines are arbitrary divisions of a single cluster):

a) (Letters a-g refer to areas marked on Fig. 26). *P. c. dalli*, smallest and highest-spired of all *P.* (*Poecilozonites*).

b) *P. c. multispira*, slightly larger at a whorl, slightly less in spire height. (The fact that *P. c. multispira* attains a large size by uniquely high whorl number does not enter the analysis, since *P. cupula* samples are standardized at $5^{3}/_{8}$ whorls.)

c) All other *P. cupula* with the exception of possible hybrids and the Devil's Hole local population of *P. c. triangularis*.

d) i) *All* proposed hybrids between *P. cupula* and *P. bermudensis*.

ii) Devil's Hole local population of *P. c. triangularis* (lowest-spired of all *P. cupula*, third largest among non-hybrids).

iii) The three *smallest* samples of *P. bermudensis zonatus*, all from the Shore Hills Formation (Nos. 2–4).

[1] Smallest in size at a whorl. This is a standardized matrix in which the effects of absolute magnitude are removed.

e) With the exception of the samples in group d, the smallest *P. bermudensis* populations.

i) The largest Shore Hills *P. bermudensis* population (*P. b. zonatus* from Government Quarry, locality 5).

ii) The lowest-spired Shore Hills *P. bermudensis* population (*P. b. fasolti* from Tom Moore's Caves, locality 53).

iii) The smallest St. George's populations of *P. b. zonatus*.

f) "Normal" *P. bermudensis zonatus*.

i) *All* eolianite samples of *P. b. zonatus*.

ii) The largest St. George's samples of *P. b. zonatus*.

iii) The smallest and highest-spired paedomorphs (5 of 6 samples of modern *P. b. bermudensis*).

g) *P. bermudensis* paedomorphs: All paedomorphic *P. bermudensis* samples with the exception of the *small P. b fasolti* and the *high-spired* modern *P. b. bermudensis*. The single modern sample of *P. b. bermudensis* of this group (Crawl Point, locality 81) is the lowest-spired and next-to-largest of recent forms.

Thus, the standardized measures of size and shape control patterns of relative similarity among samples. The extreme samples are, respectively, the smallest and relatively highest form and the largest and lowest-spired. Progression within the array is completely compatible with this interpretation; no exceptions to the even transition from small, high-spired to large, low-spired forms are found. All proposed hybrids occupy a "buffer zone" in the array of form, separating all *P. cupula* from all *P. bermudensis*.

XI. CONCLUSION

To many medieval thinkers, man was a microcosm of the creation, "the complete abridgement of the whole universe . . . a living emblem and hierogliphick of eternity and time" (Jacob Boehme, quoted in Adams, 1938: 67). Needless to say,

the Bermudian evolutionary microcosm exhibits not nearly so complete a correspondence to its macrocosm of the total history of life on earth. As I have learned from my work on allometric growth, increase in size is sufficient in itself to expose organisms to new sets of forces requiring new adaptive responses. So foreign to our experience are the forces governing a bacterium's world, that D'Arcy Thompson concluded his famous chapter "On Magnitude" with these words (1942: 77): "The predominant factors are no longer those of our scale; we have come to the edge of a world of which we have no experience, and where all our preconceptions must be recast."

Many phenomena of the Bermudian microcosm represent processes which are important in micro-evolutionary events but of little significance in the long-term phyletic history of major lineages. Random evolutionary change—the proposed initiation of infraspecific diversity in *P. cupula* according to the founder principle—does not produce the adaptive and progressive changes in form that characterize the evolutionary history of higher taxa. In another example, morphological adaptations in the phyletic history of *P. b. zonatus* may be purely phenotypic; trends involving much longer time spans and more profound alterations of form will always have a genetic basis. In more general terms, micro-evolutionary studies focus on the production of diversity in response to isolation and environmental differences. The extrapolation of these emphases leads to a "species divergence model," which views the evolution of higher taxa as a simple extension of microcosmic processes of speciation—i.e., the higher taxon is viewed as a larger branch on the traditional tree, the boughs and branches of which continually diverge. This extrapolation does not give sufficient emphasis to the massive parallelism and trends toward increased mechanical efficiency that proceed in a relatively constant physical environment. These are major determinants of patterns in transspecific evolution but have little relevance to phenomena of infraspecific variation.

In spite of this, the microcosm is a proper place to begin, for only here can the variables be sufficiently limited to permit an unambiguous tracing of actual evolutionary histories rather than possible structural sequences (which always involve the application of *a priori* hypotheses concerning the most probable routes of evolutionary change). Moreover, some aspects of the history of *Poecilozonites*—in particular, the four-fold iterative paedomorphosis of *P. bermudensis*—involve the repetitive occurrence of adaptive events, an outstanding feature of the macrocosm not often recorded at the level of infraspecific diversity. These repetitive events have a special importance in paleontology that is not often realized. Paleontology, when it deals with the documentation of phylogeny, operates in the realm of history. Simpson notes that "historical events are unique, usually to a high degree, and hence cannot embody laws defined as recurrent repeatable relationships" (1963: 29). But history becomes scientific when inductive generalizations are derived from series of events by the extraction of repetitive aspects from their integral uniqueness. By establishing a role for induction in history, repetitive occurrence leads to the formulation of laws; this is the major contribution of parallelism, convergence, and iteration to the explanation of evolutionary events—for explanation involves subsumption of observed conditions under general laws. As Harris and Morren (1966: 127) have noted for the related field of sociocultural evolution: "Convergences and parallelisms . . . are the prime source of evidence for the existence of regular and lawful selective processes in sociocultural evolution. In them reside the chief natural substitute for laboratory controls and the greatest hope for the formulation of operationally valid theories of sociocultural causation."

To obtain the detail required for unambiguous documentation of evolutionary events, we sacrifice the extensive time, geography and morphological change of major chapters in the history of life. An expert, it is said, is one who knows more and more about less and less. Our hope, however, is that such limitation will enable us to establish general principles which, although undiscoverable in the "more and more" of space, time, and morphology, are applicable to it.

XII. SUMMARY OF ARGUMENTS

1. Introduction

1a. The extreme limitation of time and space attained in studying the Bermudian Pleistocene eliminates many confusing variables that usually hinder evolutionary interpretations.

1b. If the operation of evolutionary processes in time is the object of study, chronologic placement of a time segment is of no special importance. The Pleistocene presents several advantages based on good preservation and usual persistence of species in the modern fauna.

1c. Previous studies of Pleistocene pulmonates have failed to provide evidence for evolutionary events other than extinction. This is probably an artifact of confining studies to the specific level. Infraspecific patterns of variation must be considered.

2. Geologic and Biological Background

2a. The stratigraphic column of Pleistocene Bermuda is an alternating sequence of interglacial carbonates (dunes and shallow water limestones) and glacial red soils. Snails are most common in red soils and unindurated zones of the eolianites.

2b. At the peak of its Pleistocene diversity, *Poecilozonites* contained three subgenera and 15 species varying from 5–45 mm in width and occupying a broad range of ecologic roles—a classic case of insular divergence after chance introduction to an area free from competitors. High stands of interglacial seas and the later introduction of pigs, rats, and other pulmonates by man have reduced this diversity drastically.

2c. This study deals with all taxa of one of the three subgenera—*P.* (*Poecilozonites*).

3. Quantification

3a. There are two major roles for quantitative data in this study: i) Comparisons among variables: Redundancies can be eliminated and the causal factors of association among variables (in ontogeny and phylogeny) inferred.

ii) Comparisons among samples: Since allometry is so pervasive in the ontogeny of these pulmonates, samples can be properly compared only when all the variables characterizing them have been standardized at a common size or whorl number. The standardized "matrix of means" provides the data for objective multivariate comparisons among variables.

3b. Forty-four raw and derived variables are defined, including measures of color and thickness, as well as those of size and external shape. These allow a fairly complete reconstruction of the shell from their values alone and should encompass the significant dimensions of metric variability.

4. Ontogeny of P. (Poecilozonites)

4a. The ontogenetic relationship between each variable and shell size is allometric.

4b. Ontogeny of color: Intensity of coloration increases with growth as the intermittent blotches of early ontogeny coalesce to form a band and the bands increase in relative width.

4c. Ontogeny of shape: Allometric trends in shape are determined by several factors and may be complex. The protoconch is a nucleus about which the early whorls must be molded. The primary control of later growth is exerted by doming of the spire, largely produced by increasing relative height of the aperture.

5. *Interrelationship of Variables*

5a. The interrelationship of variables is approached by factor analysis, which discerns clusters of variables by the projection of their vectors onto a small number of reference axes.

5b. The following clusters were obtained in an 8-axis solution for a *P. bermudensis* sample from locality 5 (25 specimens, 45 variables, size range 23.2–37.8 mm): size (most non-standardized raw variables), form ratio, standardized widths and heights, color.

5c. Successive reduction of factor axes produces a hierarchy of relative size independence. More and more variables are incorporated into the size cluster (even standardized widths are weakly related to size) until, in a 2-axis solution, only standardized heights retain their separate sorting.

5d. Ten other analyses yield similar results. The smaller the size range of the sample, the weaker the controlling influence of absolute size upon variable interrelationships. Several variables are redundant: total width at the first whorl, for example, is always tied to protoconch width.

6. *Evolution of* P. cupula

6a. Three species of previous authors and two forms that would have merited specific status under criteria previously used are constituted as subspecies of *P. cupula*. Each occupies a unique segment of the species' geographic range and has a non-disjunct temporal distribution—thus satisfying criteria for a biological subspecies. In particularly favorable cases, the biospecies is an operational concept in paleontology.

6b. *P. c. cupula,* largest among *P. cupula* at the fifth whorl, probably evolved from *P. c. cupuloides* by stabilization of one morph of the latter's four-fold polymorphism. In polymorphic *P. c. cupuloides*, shells of this morph are significantly larger than those of others. Moreover, shells of *P. c. cupuloides* from populations which have stabilized the three other morphs are smaller than those of *P. c. cupula* or of the *cupula*-like morph of *P. c. cupuloides*. This pervasive correlation of color and size suggests that color variation, often so difficult to interpret in adaptive terms, may be a pleiotropic concomitant of other selected characters.

6c. The diversity of *P. cupula* can be related to sea level changes in the Pleistocene history of Bermuda. The main period of diversification (three new subspecies) is coincident with a high sea stand (plus five meters) that dissected Bermuda into a large number of isolated islands; the extinction of the species (four subspecies) is related to a higher sea (plus 20 meters), that virtually inundated the entire land mass.

6d. The role of random evolutionary factors (genetic drift and the founder principle) has been the focus of a major debate among pulmonate specialists. The demonstration that selection *could* serve as a completely sufficient cause of differences among populations need not prove that it *does* so serve. The reduced color variability of one or a few chance founders probably played a role in the stabilization of morphs in post-Walsingham populations of *P. c. cupuloides*.

7. *Evolution of the* P. nelsoni *Stock*

7a. Of five subspecific names available in the typological compendium of shapes that formed the previous classification of *P. nelsoni*, four fail to meet criteria for biological subspecies. All four occur in red soils, but their sporadic distribution in space and lack of morphological distinctness suggests one single, highly variable taxon—*P. n. nelsoni*.

7b. The fifth, *P. n. callosus*, is smaller, more weakly colored and thicker shelled than *P. n. nelsoni*. Moreover, it has a distinct geographic distribution, being confined to eolianites.

7c. In two red-soil localities, a closely

related form is found with *P. n. nelsoni*. This is a new species (presumed sympatry without interbreeding)—*P. superior superior*. This species also has a thicker-shelled and more weakly-colored eolianite counterpart, *P. s. arenicolus*. The *P. nelsoni* stock is composed of two species, each with a red-soil and an eolianite subspecies.

7d. The eolianite subspecies of both species share common features, independently developed of course, which can be interpreted in adaptive terms. The thick shell is related to the availability of lime, while weaker coloration, as Rensch has suggested, may better reflect sunlight in the highly illuminated white dune environment, or may serve a cryptic function.

7e. The vertical sequence *nelsoni-callosus-nelsoni* (Shore Hills red soil, Harrington-Pembroke eolianite, St. George's red soil) does not represent zig-zag evolution, but rather the incomplete record of two subspecies tied to environments that migrated back and forth over the Bermuda platform in response to shifting sea levels of the glacial period.

8. *Phyletic Branching in* P. bermudensis

8a. Paedomorphic populations of *P. bermudensis* are found in four distinct spatio-temporal regions of Pleistocene Bermuda. They are essentially scaled-up replicas of juvenile shells of the central stock, *P. b. zonatus* (Pl. 4, figs. 1–6).

8b. Each of these four populations represents an independent episode of paedomorphosis.

8c. Each paedomorph is a distinct genetic entity, not a mere phenotypic response to a recurrent set of environmental conditions. Each paedomorph has the geographic distribution of a peripheral isolate, and each has lost genes for previously adult features that could never be brought to phenotypic expression.

8d. Paedomorphosis has occurred by a prolongation of rapid juvenile growth rates to later sizes.

8e. The most intense episodes of paedomorphosis occurred in red soils, less intense in unindurated zones and none in carbonate dunes. Paedomorphosis is one pathway (of several taken by various *Poecilozonites* taxa) to the development of thin shells in the low calcium environment of red soils.

9. *Phyletic Evolution of* P. bermudensis zonatus

9a. The relationship of form and environment in pulmonates has been a subject of debate since Darwin's time. For reasons related both to their ideas of evolution and their larger world view, Gulick and Crampton denied the environment a major role, but the modern evolutionary synthesis has reasserted the importance of environment in setting the direction of natural selection.

9b. The Bermudian stratigraphic sequence reflects a two-stage oscillation of glacial (red soil) and interglacial (marine and dune carbonate) conditions. Zig-zag trends in the morphology of *P. b. zonatus* correspond to the alternation of environments (Figs. 23, 24). Shells are thin and small-at-a-whorl in red soils, thick and large-at-a-whorl in eolianites.

9c. These trends are the same as those noted for modern pulmonates in a similar range of environments. The trends are clearly adaptive. Particularly strong is the correlation of shell thickness and availability of lime for seven independent events in several taxa of *P.* (*Poecilozonites*).

9d. It is one of the frustrations of such work that, while we can affirm the adaptive nature of a correlation between climate and morphology, we cannot tell whether we are dealing with genetically determined changes or purely phenotypic responses.

10. *Interspecific Hybridization:* P. cupula-P. bermudensis

10a. *P. cupula* and *P. bermudensis*, although sympatric, apparently did not occupy the same habitat. When brought into direct contact, the two species hybridized. Two populations, intermediate in

form and exhibiting the complete color range from "pure" *cupula* to "pure" *bermudensis* are interpreted as hybrids (Pl. 5).

10b. Two varimax factor axes account for 95.7 per cent of all information of all samples of the two species. The 57 samples (each based on 25 standardized variables) are arranged in roughly linear order varying from the smallest and highest-spired form (*P. cupula dalli*) to the largest and lowest-spired (*P. bermudensis* paedomorphs). No exceptions to the even transition from one extreme to the other are found within the array. All hybrids occupy a "buffer zone" separating all *P. cupula* from all *P. bermudensis*.

NOTES ADDED IN PROOF

Since this work was written and processed at the pace traditionally identified with its zoological subject, I hasten to add some new information of the last two years:

1. The correlation of wide protoconch, intense coloration and height of later whorls, noted and puzzled over in Chapter 5, has now been affirmed for two species of the subgenus *P.* (*Gastrelasmus*). G. Edynak, working with my assistance but without my prompting (as I had quite forgotten about the result), obtained R-mode clusters of protoconch width, late heights and color flame widths in both *P. blandi heilprini* and *P. reinianus vanattai* (Shore Hills Soil, Prospero's Cave). An intensified developmental (metabolic?) rate might produce all these features—large protoconchs (in large eggs), strong doming, and more complete coverage of the shell surface with color flames.

2. An inference that I termed "very speculative" and "tenuous" turns out to be false. *P. cupula triangularis* did not arise at the base of the Harrington. I have now found it in a Walsingham unindurated zone on the Air Base and in the Shore Hills soil in the city of Hamilton.

3. The morphologic oscillations of *P. b. zonatus* in western Bermuda, shown in Figures 23 and 24, were not well established because the St. George's points were based upon one sample only. I have since found another exposure of St. George's soil at the south end of Ireland Island and am pleased to report that 10 specimens yield an average value of .126 mm for callus thickness and 14.52 mm for size at fifth whorl. Both are much smaller than any comparable value for any eolianite sample of *P. b. zonatus*.

4. A study of microgastropod form and frequency (to be published in the proceedings of the 1969 North American Paleontological Convention) has elucidated some reasons for the ecological separation of *P. bermudensis* from *P. cupula* and *P. nelsoni* and for the extinction of the latter two. *P. cupula* and *P. nelsoni* are not found with gastropod assemblages that indicate warmth and dryness, just those conditions associated with the high Spencer's Point sea that heralded their demise.

5. The microgastropod study has provided several more correlations of form and diversity with Pleistocene climates. *Thysanophora hypolepta* and *Carychium bermudense* display oscillating trends in morphology, but their adaptive significance is unclear. Availability of $CaCO_3$ is again a controlling factor. The non-calciphilic *Thysanophora hypolepta* dominates red soil samples, but calciphilic species of *Gastrocopta*, *Carychium*, and *Vertigo* dilute its relative abundance in eolianites.

6. I have located the type of *P. cupula dalli*, mixed among related material in the collections of the United States National Museum, Washington, D.C. It has been recatalogued and given the number U.S.N.M. 679536 (Division of Mollusks). Its coloration ($02^{n}3$) and form clearly ally it with the Albuoy's Point sample, but the more angulate periphery and higher spire (though, I suspect, not a stronger dome) are beyond the variability range of Albuoy's Point and suggest a separate local population of *P. c. dalli*. Moreover, the matrix indicates a red soil cave filling (and therefore almost surely Shore Hills—I know of no St. George's cave deposits that have yielded fossils). This

finding removes the somewhat disturbing datum that *P. c. dalli* had been the only taxon of *Poecilozonites* known from a single locality. But it also invalidates (along with the new *P. c. triangularis* data of this addendum) my tenuous inference associating origin of several subspecies with the Devonshire sea stand. However, my firmer conclusion, that all subspecies were extinguished during the Spencer's Point high sea stand, has been strengthened by the discovery of many new St. George's and Southampton localities, none of which contain a trace of *P. cupula*.

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Appendix I:

SYSTEMATICS

These skeleton descriptions contain only the basic information of type repository and locality, morphology, and distribution. The details of morphological distinction are summarized in the matrices of means, Appendix 3.

Class: Gastropoda

Subclass: Pulmonata

Order: Stylommatophora

Family: Zonitidae

Subfamily: Poecilozonitinae Pilsbry, 1924

Genus: *Poecilozonites* O. Boettger, 1884

Type: *Helix bermudensis* Pfeiffer, 1845, designated by Pilsbry, 1888: 286

Subgenus: *Poecilozonites* (*Poecilozonites*) Pilsbry, 1924

Poecilozonites bermudensis (Pfeiffer, 1845)

Type: *Poecilozonites bermudensis bermudensis* (Pfeiffer, 1845)[1]

Diagnosis: Shell generally larger, lower-spired, and less intensely domed than in *P. cupula;* smaller and more strongly-domed than *P. nelsoni;* coloration pattern 123 in eastern Bermuda (eastern Devonshire Parish and eastward) and 023 in western Bermuda during Shore Hills to Southampton times; recent shells all 123; band margins diffuse in 123 form, fairly sharp in 023 shells; supplementary color wash usually present below band 3; relative width of band 3 invariably greater than in *P. cupula;* "faded" variation (bands replaced during ontogeny by lines at the band peripheries) present in all 123 samples save *P. b. fasolti* and *P. b. bermudensis;* parietal callus present in *P. b. zonatus*, *P. b. siegmundi*, and *P. b. sieglindae;* strongly angulate at periphery of the fifth whorl.

Distribution: Island-wide. Shore Hills-Recent.

Poecilozonites bermudensis zonatus Verrill, 1902

Plate 4, nos. 1 and 2. M.C.Z. Nos. 28987 and 28988

Poecilozonites bermudensis zonata—Verrill, 1902, Trans. Conn. Acad. Arts Sci., v. 11, p. 728 (footnote; no figure). Formally described in Verrill, 1905, Trans. Conn. Acad. Arts Sci., v. 12, pp. 164 and 191 as (emend.) *Poecilozonites bermudensis zonatus.* Holotype and paratypes figured in Verrill, 1905, plate 27, figure 2. Localities not specified; both eastern and western snails are figured. I have not been able to locate the actual type specimens.

Description: Color pattern is 123 in eastern Bermuda, 023 in western Bermuda; generally, all bands have formed by the fifth whorl; highest-spired, most strongly-domed and relatively highest of *P. bermudensis* subspecies; umbilicus relatively narrow for the species; parietal callus well developed; aperture relatively high and

[1] Repository of types not specified. The identity, based on illustrations of Pfeiffer's shells in Reeve (1854), is beyond doubt.

rounded in outline; size at fifth whorl spans entire range for species; 5 1/4 to 6 2/4 postprotoconch whorls at maximum (only Shore Hills samples exceed 6 whorls).

Distribution: Island-wide. Shore Hills-Southampton.

Poecilozonites bermudensis fasolti new subspecies

Holotype: Plate 4, no. 3. M.C.Z. No. 28989

Holotype from locality 53, Tom Moore's Caves, Hamilton Parish, Shore Hills Soil.

Description: Color pattern 1^f2^f3; flame-band transition occurs after fifth whorl and is rarely seen at all; spire very low and weakly domed, making *P. b. fasolti* the relatively widest subspecies of *P. bermudensis;* umbilical width maximum for species; parietal callus never developed; aperture relatively high (though lower than Shore Hills *P. b. zonatus*), with angular outlines; small at fifth whorl, as in all Shore Hills *P. bermudensis:* 6 postprotoconch whorls at maximum.

Remarks: Paedomorphic offshoot of Shore Hills *P. b. zonatus.*

Distribution: Known from a single locality, Tom Moore's Cave, Hamilton Parish. Shore Hills Soil.

Poecilozonites bermudensis siegmundi new subspecies

Holotype: Plate 4, no. 4. M.C.Z. No. 28990

Holotype from locality 10, southern tip of Ireland Island, Sandys Parish, Harrington Formation.

Description: Color pattern 023, with band formation occurring later in ontogeny than in typical western *P. b. zonatus;* spire low and weakly domed but relatively highest among the paedomorphic subspecies of *P. bermudensis;* umbilicus moderately wide; parietal callus weakly developed; aperture relatively low with angular outline; large at fifth whorl; 5 to $5^{6}/_{8}$ postprotoconch whorls at maximum.

Remarks: Paedomorphic offshoot of western *P. b. zonatus.*

Distribution: Southern end of Ireland Island, Sandys Parish, Harrington Formation.

Poecilozonites bermudensis sieglindae new subspecies

Holotype: Plate 3, no. 5, M.C.Z. No. 28991

Holotype from locality 44, Rocky Bay, Devonshire Parish, Harrington Formation.

Description: Color pattern 123, with band formation occurring later in ontogeny than in typical eastern *P. b. zonatus;* spire low and weakly domed; umbilicus wide; parietal callus weakly developed; aperture relatively low with angular outline; large at fifth whorl; 5 to $5^{6}/_{8}$ postprotoconch whorls at maximum.

Remarks: Paedomorphic offshoot of eastern *P. b. zonatus.*

Distribution: Rocky Bay, Devonshire Parish, Harrington-Pembroke Formations.

Poecilozonites bermudensis bermudensis (Pfeiffer, 1845)

Plate 4, no. 6. M.C.Z. No. 28992

Helix bermudensis—Pfeiffer, 1845, Proc. Zool. Soc. London, v. 13, p. 67. (Complete synonymy up to 1889 given in Pilsbry, 1889a. Inclusion in *Poecilozonites* has not been questioned since then.) Pfeiffer's description lists habitat simply as "Bermuda"; no figure given. Pfeiffer's shells are figured by Reeve, 1854, plate 57. They are Recent forms.

Description: Color pattern 1^f2^f3 in St. George's-Southampton forms, often 123 in Recent shells; spire weakly domed in all forms, low in St. George's-Southampton, moderate to high in Recent forms due to increase in early whorl heights; umbilicus wide in St. George's-Southampton, moderately wide in Recent samples; callus not developed; large at fifth whorl in St. George's-Southampton, small to moderate in Recent; 5 to $5^{1}/_{2}$ postprotoconch whorls at maximum.

Remarks: Paedomorphic offshoot of eastern *P. b. zonatus.*

Distribution: Confined to St. George's Island. St. George's Parish in St. George's-Southampton times. Island-wide at present.

Poecilozonites nelsoni (Bland, 1875)

Type: *Poecilozonites nelsoni nelsoni* (Bland, 1875)

Diagnosis: Shell larger, dome more triangular in cross section than other taxa of subgenus; color pattern 123 or 023; parietal callus weakly developed in red soils, strong in eolianites; 7 to 8 postprotoconch whorls in large specimens; distinguished from *P. cupula* and *P. bermudensis* by larger size, whorl number, and weakly-domed spire and from *P. superior* by lower spire, weaker dome, and strength of second color band.

Distribution: Shore Hills-St. George's. Island-wide.

Poecilozonites nelsoni nelsoni (Bland, 1875)

Plate 2, nos. 1–7

Hyalina nelsoni Bland, 1875, Ann. Lyceum Nat. Hist. New York, vol 11, p. 78. Locality listed as "Bermuda," repository of types unspecified.

Poecilozonites nelsoni var. *discoides* Gulick, 1904, Proc. Acad. Nat. Sci. Phila., p. 416. Locality listed as "large quarry 1/2 way bet. Tuckerstown and Walsingham." Shore Hills soil. Holotype: Plate 2, no. 1 (A.N.S.P. No. 58084).

Poecilozonites nelsoni conoides Verrill, 1905, Trans. Conn. Acad. Arts Sci., p. 163. Locality listed as "near the western shore of Castle Harbour in a mass of red-clay and stalagmite," Shore Hills soil. Topotype: Plate 2, no. 4 (M.C.Z. No. 29013).

Description: Color pattern 123 with diffuse band margins (023 with sharper margins in Shore Hills samples from Sandys Parish); spire low (Gulick's rejected *P. n. discoides*) to high (Verrill's rejected *P. n. conoides*); rather triangular in cross section; protoconch and size at fifth whorl largest for subgenus; maximal size (77.6 mm) and postprotoconch whorl number (8) for subgenus; callus absent or weakly developed; umbilicus relatively wide in most samples; rounded to angulate at fifth whorl periphery.

Distribution: Shore Hills-St. George's. Island-wide in Shore Hills, Smiths Parish in Harrington-Pembroke, Hamilton and St. George's Parish in St. George's.

Poecilozonites nelsoni callosus Gulick, 1904

Plate 3, nos. 1–3

Poecilozonites nelsoni var. *callosus* Gulick, 1904, Proc. Acad. Nat. Sci. Phila., p. 416. Locality listed as "Benj. Trott's sand pit Tucker's Town," from unindurated zone presumably Harrington in age. Holotype: Plate 3, no. 2 (A.N.S.P. No. 58086).

Description: Color pattern 023 with sharp band margins; spire medium in height, rather triangular in cross section; smaller than *P. n. nelsoni* in maximal size, whorl number, protoconch width, and size at fifth whorl; shell thick with strongly developed parietal callus; umbilicus usually constricted by shell thickening; angulate at periphery of fifth whorl.

Distribution: Harrington-Pembroke in eastern Bermuda.

Poecilozonites cupula Gulick, 1904

Type: *Poecilozonites cupula cupula* (Gulick, 1904)

Diagnosis: Shell generally smaller and higher-spired than other members of subgenus; distinguished from *P. bermudensis* by following features of coloration: different banding patterns ($12^{n}3$, $1^{f}00$, $1^{f}03$, $02^{n}3$, $1^{f}2^{n}3$), sharpness of band margins, absence of a supplementary color wash below band 3, lower relative width of band 3, and absence of the "faded" variation; differs from *P. nelsoni* and *P. superior* by smaller size and generally stronger dome; parietal callus lacking in all subspecies; faintly to moderately angular at periphery of the fifth whorl.

Distribution: Walsingham-Pembroke in eastern Bermuda. No specimens known west of Devonshire Bay with exception of possible hybrid population at Fort Scaur, locality 69.

Poecilozonites cupula cupula (Gulick, 1904)

Plate 1, no. 1. M.C.Z. No. 29006

Poecilozonites cupula—Gulick, 1904, Proc.

Acad. Nat. Sci. Phila., v. 56, p. 417. Holotype, A.N.S.P. No. 58085, Department of Malacology. Locality described as "large quarry 1/2 way between Tuckerstown and Walsingham. A. Gulick, 1903!" Paratypes bear No. A.N.S.P. 85507. Shore Hills Soil.

Description: Color pattern invariably 12^n3; spire high and strongly domed (type locality, Walsingham local population) to low and moderately domed (South Shore local population); protoconch and size at fifth whorl largest among *P. cupula* subspecies; $5\frac{1}{2}$ to $6\frac{1}{2}$ postprotoconch whorls at maximum.

Distribution: Hamilton, Smiths, and southeast corner of Devonshire Parishes, Shore Hills-Pembroke.

Poecilozonites cupula dalli (Gulick, 1904)

Plate 1, no. 2. M.C.Z. No. 29007

Poecilozonites dalli—Gulick, 1904, Proc. Acad. Nat. Sci. Phila., 56: 417. Type locality unknown, repository of type unspecified. Figure and description agree entirely with Albuoy's Point sample described below.

Description: Polymorphic in color; morphs 1^f03, 02^n3 and 1^f2^n3 are known, of which the second predominates; highest and most strongly-domed spire of all samples of *Poecilozonites;* smallest protoconch and size at fifth whorl and absolutely smallest form of subgenus; umbilicus constricted due to increased intensity of doming during ontogeny; aperture relatively high and narrow; $5\frac{1}{2}$ to 6 postprotoconch whorls at maximum.

Distribution: Known from a single locality, Albuoy's Point, Smiths Parish (locality 4), Harrington-Pembroke (?).

Poecilozonites cupula cupuloides (Peile, 1924)

Plate 1, no. 3. M.C.Z. No. 29008

Poecilozonites cupuloides—Peile, 1924, Proc. Malacol. Soc. London, 16: 17. Holotype in British Museum. Paratypes at Philadelphia Academy of Natural Sciences, A.N.S.P. No. 131584, Department of Malacology, labeled "'cupuloides' (part of original lot) 80 yds. N. of Harrington House, Harrington Sd. Base of 10 ft. hard limestone road cutting. Arthur Haycock 1922!" Walsingham Formation. Holotype displays morph 1^f2^n3.

Description: Polymorphic in color, morphs 1^f00, 1^f03, 02^n3 and 1^f2^n3; all four present in oldest Quarry Road local population, first and second stabilized in Coney Island local population, the third in Bird's Nest and Surf Bay local populations. Spire moderate in height and doming intensity; size at fifth whorl and maximal size moderate for the species; $5\frac{2}{4}$ to $6\frac{1}{4}$ postprotoconch whorls at maximum.

Distribution: Hamilton Parish, Tucker's Town, Walsingham-Shore Hills.

Poecilozonites cupula multispira new subspecies

Holotype: Plate 1, no. 4. M.C.Z. No. 29009

Holotype from locality 84, St. David's Island, St. George's Parish. Largest specimen of the sample. Harrington-Pembroke (?).

Description: Polymorphic in color; morphs 02^n3 and 1^f2^n3 are known, of which the former predominates; spire of large specimens high, but only moderately domed; strong relative height attained by addition of whorls (a large specimen may have 8 postprotoconch whorls); although maximal size is largest among *P. cupula* subspecies, size at the fifth whorl exceeds that of *P. c. dalli* only slightly (and insignificantly); 7 to 8 postprotoconch whorls at maximum.

Distribution: St. David's Island, St. George's Parish, Harrington-Pembroke (?).

Poecilozonites cupula triangularis new subspecies

Holotype: Plate 1, no. 5. M.C.Z. No. 29010

Holotype from locality 46, South Shore Road at Pink Beach, southeast corner of Smith's Parish. Pembroke Formation.

Description: Polymorphic in color; morphs 02^n3 and 1^f2^n3 are present; lowest spire, least strongly-domed and relatively

widest subspecies of *P. cupula;* as relatively widest form, fairly angulate at periphery (other subspecies of *P. cupula* very weakly carinate), but peripheral keel still not as strong as in more strongly domed *P. bermudensis;* size at fifth whorl exceeded only by *P. cupula cupula*; 5 to 5^{6}s postprotoconch whorls at maximum.

Poecilozonites superior new species

Type: *Poecilozonites superior superior* new subspecies

Diagnosis: Shell large and strongly domed with high spire; color 123 with sharp band margins, $12^{n}3$ or 103; parietal callus absent or weakly developed even when shell thick; 7 to 8 postprotoconch whorls in large specimens; distinguished from *P. bermudensis* by color and larger size and whorl number, from *P. cupula* by larger size and whorl number, from *P. nelsoni* by color, higher spire, and stronger dome.

Distribution: Shore Hills-Pembroke, eastern Bermuda.

Poecilozonites superior superior new subspecies

Holotype: Plate 2, no. 8. M.C.Z. No. 29016

Holotype from locality 5, Government Quarry (Bird Fissure), Shore Hills Soil.

Description: Color pattern 123 with sharp band margins; spire high and strongly domed in cross section; smaller and fewer whorls at final size than in *P. nelsoni*; shell thin; callus absent or weakly developed; umbilicus constricted by increase in spire height in ontogeny; rounded at fifth whorl periphery.

Distribution: Shore Hills, Hamilton Parish.

Poecilozonites superior arenicolus new subspecies

Holotype: Plate 3, no. 4. M.C.Z. No. 29019

Holotype from locality 11, Ferry Road north of Biostation, Pembroke eolianite.

Description: Color pattern $12^{n}3$ or 103; spire high and strongly domed in cross section; protoconch generally smaller than in *P. n. nelsoni* or *P. s. superior;* shell thick but callus still absent or weakly developed; umbilicus constricted by spire height and shell thickening; faintly angulate to rounded at fifth whorl periphery; up to 8 whorls at final size.

Distribution: Shore Hills to Pembroke, eastern Bermuda.

Appendix 2:

REGISTER OF LOCALITIES

Localities are described in numerical order. Following the descriptions, locality numbers are listed by parish and by subspecies. Only localities mentioned in the text are described. I shall be glad to furnish a more detailed list to any enquirer.

1. Northern end of Whalebone Bay. Harrington unindurated zone, averaging two feet in thickness, overlies Devonshire sands and veneer of intertidal conglomerate. Shore Hills soil stripped away for the most part, but preserved in "palmetto stumps," solution pipes in the massive Belmont marine limestone. Snails from Harrington and base of overlying Pembroke eolianites.

2. South shore on promontory west of Devonshire Bay. Harrington unindurated zone overlies well-developed Devonshire intertidal marine conglomerate covering massive Belmont marine limestone. Leeward beds of a Pembroke dune overlie Harrington.

3. North Shore Road, first bus stop northwest of Flatts on road to St. George's. North side of road. A one-foot thick exposure of Shore Hills soil is overlain by a foot of pinkish Harrington deposition. No intervening Devonshire, since area is topographically above maximum extent of Devonshire sea. Hybrids of *P. c. cupula* and *P. b. zonatus*.

4. Albuoy's Point, road cut north of

South Shore Road. *P. c. dalli* in unindurated zone.

5. Government Quarry. Numerous fissures in Walsingham eolianite filled with Shore Hills soil. Each fissure has a distinct fauna; they are almost surely of different ages. *P. b. zonatus* in Graveyard Fissure (mostly quarried away by 1967), *P. n. nelsoni* and *P. b. zonatus* in Main Fissure (south wall of quarry), *P. n. nelsoni* and *P. s. superior* in Bird Fissure (quarried away), and *P. n. nelsoni* in Coquina Fissure (west wall).

6. Black Watch Pass. *P. b. zonatus* in unindurated zone (Harrington or Pembroke) at the base of the road cut at the north end of Black Watch Pass. Zone rises to south.

9.[1] Harrington Sound Road at northern entrance to Government Quarry. *P. c. cupuloides* in poorly-developed intra-Walsingham red soil exposed on erosional high, and in Walsingham eolianite above. A single *P. n. nelsoni* or *P. s. superior* from a Shore Hills-filled Walsingham fissure.

10. Southern tip of Ireland Island. Type locality of *P. b. siegmundi*. Poorly-developed Harrington unindurated zone overlies Devonshire eolianite that can be traced to typical Devonshire intertidal conglomerate on the northwest coast.

11. Ferry Road, north of Biostation. Thin deposits of Shore Hills and St. George's soils with Pembroke eolianite between. *P. s. arenicolus* in Shore Hills and Pembroke; *P. b. bermudensis* in overlying Southampton eolianite.

12. Mullett Bay Road. St. George's soil on erosional high exposed for 10 meters along the road, diving beneath road level at each extremity of the outcrop. A few *P. b. bermudensis*.

15. Sand pit in golf course of St. George's Hotel. An unindurated zone in Southampton eolianite. Type locality for Sayles's (1931) rejected "McGall's soil."

16. Mullett Bay Road just before entrance to St. George's Towne. Good development of St. George's soil on erosional high. Type St. George's with a few *P. b. bermudensis*.

17. Abandoned railroad cut east of Whalebone Bay. Good exposure of Pembroke and Southampton eolianites with strong St. George's profile (1/2 to 3 feet thick). *P. b. zonatus* in St. George's and at several levels in the Southampton.

18. Abandoned railroad cut west of Tank Farm Pier. *P. n. nelsoni* in St. George's soil, filling fissure in Pembroke eolianite.

21. Quarry cut between Mullet Bay Road and abandoned railroad cut exposing Southampton dune. *P. b. bermudensis* found at three levels: in, above (eolianite), and below (eolianite) a brownish unindurated zone. Lower eolianite is locality 21a; upper is 21d.

24. Khyber Pass, Signal Hill. Unindurated zone (averaging 3 feet in thickness) in a Southampton dune. Type locality of Sayles's (1931) rejected "Signal Hill Soil."

27. Tobacco Bay. *P. b. bermudensis* in loosely-consolidated Southampton eolianite.

28. East coast of St. George's Island at Buildings Bay. Good development of Harrington Formation containing only known shells of *P. b. zonatus* on St. George's Island.

30. North Shore Road at "Bird's Nest" residence. Well-developed profile of Shore Hills soil dips westward. *P. c. cupuloides* in Belmont eolianite just below the base of the Shore Hills. *P. nelsoni* in both Shore Hills (*P. n. nelsoni*) and unindurated zone of overlying (Pembroke?) eolianite (*P. n. callosus*). Only known locality in which *P. nelsoni* is found in two superposed horizons.

31. South shore, west end of Spittal Pond. St. George's soil on erosional high

[1] Missing numbers correspond to collecting localities that either yielded no *Poecilozonites* or provided specimens not discussed herein.

atop Pembroke dune covering Shore Hills deposits.

32. South shore, east of Spanish Rock. Unindurated zone in Pembroke dune.

34. Wilkinson's Quarry. Very strong development of Shore Hills soil. *P. n. nelsoni* in several Shore Hills fissures within Walsingham eolianite. One fissure (south wall) has both *P. n. nelsoni* and *P. s. superior*.

35. South shore at deep inlet east of Spencer's Point. Unindurated zone in Pembroke dune, may be correlative with locality 32. *P. c. cupula*.

36. Quarry south of South Road, north of Spencer's Point. *P. b. zonatus* in massive, poorly-consolidated upper Southampton eolianite.

37. South shore, western end of McGall's Bay. *P. b. zonatus* in thin layer of St. George's soil overlying Spencer's Point intertidal marine conglomerate.

39. South shore at eastern end of Saucos Hill. *P. c. cupula* in whitish well-developed unindurated zone and in overlying eolianites. Harrington-Pembroke interval.

40. North slope of Saucos Hill south of South Road. *P. b. zonatus* in barely consolidated late Southampton eolianite.

41. South shore at western end of Saucos Hill. Most complete superposed sequence on Bermuda. *P. c. cupula* in Harrington-Pembroke unindurated zone correlating with that of locality 39. *P. b. zonatus* in poorly-developed St. George's soil and in massive overlying Southampton eolianites.

43. South shore on northeast end of peninsula west of Sue Wood Bay. *P. c. cupula* in unindurated zone correlating with that of localities 39 and 41.

44. South shore on promontory west of Rocky Bay. Type locality of *P. b. sieglindae*, found in Harrington unindurated zone and overlying Pembroke eolianite.

45. Harrington Sound Road just west of Sharks Hole. Unindurated zone at road level, *P. nelsoni callosus* fairly common. Sayles's type Harrington, but may be a Pembroke unindurated zone.

46. South Road just east of Pink Beach. Type locality of *P. c. triangularis*. A well-developed Harrington-Pembroke unindurated zone exposed in a road cut, north side of road.

47. South shore at Cox's Bay. St. George's erosional surface reaches Belmont marine limestone just east of locality. St. George's rises westward over a Pembroke dune containing *P. b. zonatus*.

48. Ferry Road, halfway between Biostation and Whalebone Bay. *P. c. cupuloides* in thin exposure (less than 1 foot) of Shore Hills soil.

49. South shore just west of Hungry Bay. Well-developed brownish Harrington unindurated zone overlies Devonshire intertidal conglomerate. Devonshire fills wave-cut notch on western end of Hungry Bay.

51. South shore at Grape Bay. Second most complete superposed sequence on the island. Shore Hills soil present in solution pipes and as veneer on Belmont conglomerate. Thick intertidal Devonshire conglomerate follows, overlain by Devonshire sands and brown Harrington unindurated zone with *P. b. zonatus*. Leeward beds of a Pembroke dune follow, capped by the St. George's erosional surface.

53. Cave north of Tom Moore's Tavern. Well-developed Shore Hills soil profile within cave; type locality of *P. b. fasolti*.

55. Charles Island. Well-developed unindurated zone surrounds entire island. Richest locality on Bermuda for *P. b. zonatus*. Harrington or Pembroke, since red soil overlies unindurated zone at east end of island.

56. North shore north of intersection of North Shore Road and Coney Island Road. Shore Hills soil exposed on top of eroding cliff.

62. South shore at Simmons Beach. Massive accumulation of Southhampton eolianites, with unindurated zones separating

dunes. Three superposed layers containing *P. b. zonatus*.

63. North shore south of Gibbet Island. *P. cupula cupula* in Pembroke unindurated zone at top of cliff. *P. s. arenicolus* in unindurated zone below, at sea level.

64. South Shore Road at McGall's Hill. *P. n. nelsoni* in Harrington soil exposed at road level on south side of road.

65. North shore of Ireland Island. Shore Hills soil with *P. nelsoni nelsoni* filling Walsingham fissure.

66. Quarry on southern Ireland Island. Moderately developed St. George's soil with *P. b. zonatus*.

67. Middle Road south of Wilson's Island. *P. b. zonatus* in well-developed unindurated zone of unknown age.

68. North shore north of Coney Island Road just west of Coney Island. *P. nelsoni nelsoni* in veneer of St. George's soil superposed above section containing Belmont eolianites. Shore Hills soil and Pembroke eolianites.

69. Somerset Road at Fort Scaur. (?) Hybrid *P. bermudensis* and *P. cupula* in brown soil of unknown age exposed in road cut on east side of road.

71. Surf Bay. Patchy unindurated zone separating two eolianites. Red soil (probably Shore Hills) 4 feet above. Belmont eolianite (?).

73. Sand Quarries west of Middle Road. *P. b. zonatus* in massive deposits of poorly-consolidated upper Southampton eolianites.

75. South Shore Road just east of Horseshoe Bay. *P. b. zonatus* in massive deposits of poorly-consolidated upper Southampton eolianite exposed at south side of road. Similar deposits with abundant land snails throughout this region.

76. Intersection of Knapton Hill Road and South Road. *P. c. cupula* in unindurated pocket.

77. Knapton Hill Road at crest of Knapton Hill. *P. c. cupula* in poorly-developed unindurated zone exposed in road cut.

78. Grounds of Bermuda Biostation. Living *P. b. bermudensis* in garden of "Big Wind" cottage.

79. Government Hill Road south of ruined church. *P. b. bermudensis* living on weathered eolianite in gardens along west side of road.

80. Intersection of St. David's Road and Chapel-of-Ease lane. Empty shells of *P. b. bermudensis* found amidst decaying vegetation.

81. North Shore Road south of Crawl Point. *P. b. bermudensis* living on weathered eolianite in garden on south side of road.

82. Perfume Factory. *P. b. bermudensis* living on red soil of Perfume Factory gardens.

83. Somerset Road just south of the town of Somerset. Empty shells of *P. b. bermudensis* in gardens at roadside.

84. Lighthouse Hill Road, St. David's Island. *P. nelsoni callosus* and *P. cupula multispira* (type locality) in poorly-consolidated eolianite of uncertain age (probably Harrington-Pembroke).

85. Harrington Sound Road just east of intersection with Devil's Hole Hill Road. *P. c. triangularis* in poorly-consolidated eolianite exposed in a road cut, north side of road.

86. Paynter's Road at border of Hamilton Parish and Tucker's Town. *P. nelsoni callosus* in unindurated zone. Probably Harrington or Pembroke in age.

87. Higgs Island, Town Cut. Well-developed Harrington unindurated zone lies on patchy Devonshire conglomerate and typical Belmont marine limestone. Pembroke eolianite above. *P. b. zonatus* in continuous sequence throughout Harrington-Pembroke interval.

88. Quarry on south face of Fox's Hill, St. David's Island. *P. nelsoni callosus* and *P. c. multispira* in poorly-consolidated eolianite.

89. Prospero's Cave. Well-developed

Shore Hills Soil profile within caves; *P. nelsoni nelsoni* abundant.

91. St. David's Road south of Emily's Bay. *P. c. multispira* in poorly-consolidated eolianite exposed in road cut.

95. North Shore Road west of Bailey's Bay. *P. n. callosus* in Harrington unindurated zone and in overlying Pembroke eolianite exposed on north side of road.

97. Cambridge Beaches. *P. n. nelsoni* in extensive exposure of Shore Hills soil exposed near sea level along the western shore of Somerset Island.

100. Island west of Trunk Island in Harrington Sound. *P. s. arenicolus* in lower unindurated zone (Harrington) encircling island.

P1. "Quarry near Waterloo House, Castle Harbour. A. Gulick 1903 No. 816." *P. b. zonatus* from Shore Hills soil.

P2. "Large quarry 1/2 way between Tucker's Town and Walsingham. A. Gulick 1903!" Shore Hills soil. Type locality of *P. c. cupula* and two rejected synonyms of *P. n. nelsoni* (*P. n. discoides* and *P. n. conoides*).

P3. "Whitby, Bailey's Bay. From a cleft 2 ft. wide, 90 feet above sea level, associated with bird bones, etc. Arthur Haycock 1922!" *P. c. cupula* and *P. n. nelsoni* in Shore Hills soil.

P4. "'cupuloides' (part of original lot). 80 yards north of Harrington House, Harrington Sound. Base of 10 foot hard limestone road cutting. Arthur Haycock 1922!" Type locality of *P. c. cupuloides*.

P5. "Cave near Harrington House. H. C. Hoyt 1927!" *P. b. zonatus* in Shore Hills soil.

P6. "Castle Harbor near Harrington House." *P. b. zonatus* in Shore Hills soil.

P7. "Devonshire Marsh, Gulick's locality 818." *P. b. zonatus* from unindurated zone or eolianite. Both eastern and western color forms present with intermediates.

P8. "Benjamin Trott's sand pit, Tuckerstown, A. Gulick, 1903." Probably Harrington-Pembroke in age.

P9. "Admiral's Cave, Bermuda. Hiram Hoyt." *P. n. nelsoni* in deep red soil, almost surely Shore Hills in age.

Synopsis of localities, according to parish:

A) *St. George's Parish:* 1, 11, 12, 15, 16, 17, 18, 21, 24, 27, 48, 78, 79, 80, 84, 87, 88, 91;
B) *Hamilton Parish:* 3, 5, 9, 30, 34, 45, 53, 56, 68, 81, 82, 86, 89, 95, 100, P1, P2, P3, P4, P5, P6, P9;
C) *Tucker's Town:* 55, 71, P8;
D) *Smiths Parish:* 4, 31, 32, 35, 36, 37, 39, 40, 41, 46, 63, 64, 76, 77, 85;
E) *Devonshire Parish:* 2, 43, 44, 47, P7;
F) *Paget Parish:* 49, 51;
G) *Pembroke Parish:* 6;
H) *Warwick Parish:* 62;
I) *Southampton Parish:* 67, 73, 75;
J) *Sandys Parish:* 10, 65, 66, 69, 83, 97.

Synopsis of localities according to subspecies:

A) *P. nelsoni nelsoni*
  1. Shore Hills: 5, 9 (?), 30, 34, 65, 89, 97, P2, P3, P9
  2. Harrington-Pembroke: 64
  3. St. George's: 18, 68

B) *P. nelsoni callosus*
  1. Harrington-Pembroke: 30, 45, 84, 86, 95, P8

C) *P. superior superior*
  1. Shore Hills: 5, 9(?), 34

D) *P. superior arenicolus*
  1. Shore Hills: 11
  2. Harrington-Pembroke: 11, 63, 100, loc. ? (Bda. Museum)

E) *P. bermudensis zonatus*
  1. Shore Hills: 5, P1, P5, P6
  2. Harrington: 1, 2, 28, 49, 51, 55, 87
  3. Pembroke: 1, 6, 47, 87
  4. St. George's: 17, 31, 37, 41, 66
  5. Southampton: 17, 36, 40, 62, 73, 75

F) *P. bermudensis fasolti*
  1. Shore Hills: 53

G) *P. bermudensis siegmundi*
  1. Harrington: 10

H) *P. bermudensis sieglindae*
   1. Harrington: 44
   2. Pembroke: 44

I) *P. bermudensis bermudensis*
   1. St. George's: 11, 12, 16
   2. Southampton: 11, 15, 21, 24, 27
   3. Recent: 78, 79, 80, 81, 82, 83

J) *P. cupula cupula*
   1. Shore Hills: P2, P3
   2. Harrington-Pembroke: 32, 35, 39, 41, 43, 63, 76, 77

K) *P. cupula dalli*
   1. Harrington-Pembroke: 4

L) *P. cupula cupuloides*
   1. Walsingham: 9, P4
   2. (?) Belmont eolianite: 30, 71
   3. Shore Hills: 48, 56

M) *P. cupula multispira*
   1. (?) Harrington-Pembroke: 84, 88, 91

N) *P. cupula triangularis*
   1. Harrington-Pembroke: 46, 85

O) Hybrid *P. bermudensis-P. cupula*
   1. Shore Hills: 3
   2. Harrington: 3
   3. (?): 69

MATRIX OF MEANS FOR *P. CUPULA* (STANDARDIZED AT $5^3/_8$ WHORLS)

	ONSEUP	LOWCOL	COLOR4	COLOR5	PRDEGR	PRWIDT	PRHIGH	WIDTH1	HEIGH1
P.c. cupula									
HP35	3.812	.173	.460	.476	557.7	1.98	.355	1.93	.588
HP37	4.089	.183	.349	.425	573.5	2.04	.338	2.01	.591
HP39	4.550	.166	.355	.414	564.1	2.01	.363	1.98	.596
HP41c	4.375	.172	.341	.374	569.8	2.03	.342	2.00	.606
HP41b	4.528	.196	.357	.389	570.5	2.02	.343	1.96	.583
HP41a	4.450	.193	.323	.369	577.6	1.99	.336	1.95	.581
HP43	4.225	.188	.293	.381	562.4	2.00	.322	1.99	.567
P63		.187	.408	.436	551.1	1.98	.301	1.89	.574
SHP3	3.625	.099	.365	.440	607.9	2.09	.356	2.00	.637
SHP2	4.012	.200	.375	.459	615.7	2.25	.383	2.15	.716
P.c. triangularis									
HP46		.195	.369		544.8	1.78	.315	1.72	.515
HP85		.219	.145	.129	558.9	1.83	.319	1.81	.558
P.c. cupuloides									
W9		.170			585.6	1.91	.385	1.80	.679
WP4		.177			549.5	1.83	.389	1.78	.672
S1156		.194			597.4	1.79	.365	1.64	.603
B30		.275	.456	.427	580.7	1.85	.409	1.74	.700
SH18		.256	.194	.440	601.6	1.91	.348	1.82	.555
B71					560.7	1.78	.327	1.69	.571
P.c. multispira									
HP84 and 88		.193			558.3	1.62	.351	1.51	.574
P.c. dalli									
HP4		.191			518.3	1.52	.325	1.44	.632

	WIDTH2	HEIGH2	WIDTH3	HEIGH3	WIDTH4	HEIGH4	WIDTH5	HEIGH5	TSIZE5
P.c. cupula									
HP35	2.90	1.00	4.17	1.74	5.86	2.99	7.81	5.42	13.23
HP37	3.02	0.993	4.35	1.68	6.13	2.95	8.23	5.21	13.41
HP39	2.98	0.988	4.29	1.67	5.98	2.88	7.77	5.09	12.87
HP41c	3.01	1.05	4.32	1.78	5.95	3.15	7.91	5.60	13.51
HP41b	2.94	1.00	4.23	1.73	5.85	3.04	7.93	5.34	13.27
HP41a	2.98	0.997	4.34	1.72	6.17	3.01	8.34	5.53	13.86
HP43	3.01	1.00	4.42	1.74	6.28	3.17	7.80	5.82	13.82
P63	2.86	1.02	4.06	1.87	5.42	3.45	6.75	5.92	12.66
SHP3	2.98	1.16	4.16	2.13	5.49	3.80	6.97	6.43	13.40
SHP2	3.15	1.33	4.26	2.43	5.46	4.32	6.86	7.40	13.96
P.c. triangularis									
HP46	2.63	0.910	3.83	1.55	5.48	2.69	7.43	4.62	12.05
HP85	2.74	0.979	3.99	1.68	5.75	2.91	8.00	5.17	13.17
P.c. cupuloides									
W9	2.67	1.14	3.77	1.90	5.13	3.22	6.47	5.57	12.05
WP4	2.68	1.13	3.76	1.92	5.12	3.31	6.45	5.56	12.02
S1156	2.48	1.00	3.55	1.66	4.90	2.83	6.31	4.84	11.15
B30	2.59	1.48	3.64	1.99	4.97	3.43	6.20	5.82	12.02
SH18	2.68	0.908	3.76	1.51	5.16	2.62	6.72	4.52	11.25
B71	2.56	0.984	3.69	1.65	5.12	2.86	6.73	5.19	11.91
P.c. multispira									
HP84 and 88	2.25	0.974	3.13	1.66	4.15	2.76	5.30	4.47	9.76
P.c. dalli									
HP4	2.41	1.21	2.81	2.19	3.42	3.71	3.92	5.78	9.70

MATRIX OF MEANS FOR *P. CUPULA* (continued)

	RATIO5	PSANGL	DANGLE	KVALUE	INFORM	UMBILC	APWIDT	ALDIVW	APHIGH	RELSPI	INNLIP	OUTCAR	LOWOFF	LOWECC	UPPOFF	UPPECC	TOTECC	Total height	Total width
P.c. cupula																			
HP35	1.44	45.9	55.8	2.07	.222	1.87	8.42	1.34	6.26	.632	6.14	3.81	3.39	.403	2.94	.349	.248	9.9	17.7
HP37	1.58	43.0	55.9	2.07	.201	2.02	8.57	1.30	6.60	.667	6.33	3.87	3.86	.451	2.92	.311	.208	9.9	18.4
HP39	1.53	42.3	56.5	2.23	.181	2.08	8.25	1.28	6.43	.691	5.94	3.57	3.26	.396	2.67	.323	.281	9.3	17.5
HP41c	1.41	45.7	58.3	2.06	.239	2.08	8.32	1.37	6.07	.626	5.83	3.86	3.73	.449	3.08	.370	.181	9.7	17.7
HP41b	1.49	42.5	56.5	2.09	.216	1.89	8.12	1.34	6.18	.651	5.78	3.84	3.47	.427	2.96	.365	.208	9.5	17.7
HP41a	1.51	44.0	54.4	2.06	.218	2.03	8.73	1.31	6.66	.666	6.12	4.18	3.93	.450	3.28	.376	.174	10.0	18.4
HP43	1.37	46.2	55.2	2.10	.229	1.89	8.07	1.30	6.23	.636	5.89	3.94	3.62	.448	3.10	.384	.167	9.8	17.5
P63	1.19	57.6	58.6	2.42	.251	1.42	6.91	1.23	5.60	.571	5.51	3.32	3.43	.496	2.06	.299	.205	9.8	14.7
SHP3	1.09	55.0	60.3	2.38	.276	1.57	7.14	1.22	5.86	.548	5.71	3.63	3.41	.477	2.32	.326	.197	10.7	15.6
SHP2	0.97	56.9	63.3	2.58	.303	1.20	7.24	1.10	6.55	.516	5.69	3.80	3.68	.509	2.40	.332	.159	12.0	16.2
P.c. triangularis																			
HP46	1.61	42.4	59.1	1.94	.220	2.13	7.80	1.25	6.23	.670	5.61	3.64	3.26	.418	2.68	.314	.238	9.3	17.0
HP85	1.55	43.1	56.3	1.85	.247	1.77	8.80	1.30	6.76	.669	6.02	4.10	4.00	.455	3.50	.398	.147	10.1	18.1
P.c. cupuloides																			
W9	1.16	54.8	58.2	2.15	.282	1.34	6.92	1.18	5.86	.586	5.41	3.28	3.22	.465	2.08	.300	.235	10.0	14.9
WP1	1.16	53.8	58.2	2.19	.278	1.47	6.54	1.16	5.63	.580	5.34	3.25	2.92	.417	2.05	.313	.240	9.7	14.7
SH56	1.30	51.7	56.2	2.08	.254	1.54	6.65	1.22	5.16	.620	5.16	3.06	2.78	.417	2.07	.311	.271	8.8	14.4
B30	1.07	58.8	59.6	2.22	.296	1.45	6.57	1.17	5.64	.576	5.06	3.30	3.42	.520	2.17	.330	.149	9.8	14.2
SH18	1.48	45.2	59.4	2.19	.208	1.96	6.87	1.24	5.56	.654	5.41	3.06	2.30	.335	2.11	.308	.357	8.5	15.0
B71	1.30	53.3	60.0	2.08	.255	1.31	7.31	1.19	6.15	.627	5.59	3.52	3.45	.558	2.40	.328	.206	9.8	15.0
P.c. multispira																			
HP81 and 88	1.19	49.6	58.3	2.24	.276	1.05	5.54	1.29	4.29	.613	4.42	2.34	2.18	.393	1.39	.250	.356	7.0	12.2
P.c. dalli																			
HP4	0.68	70.3	60.3	2.95	.418	0.68	4.09	0.97	4.20	.491	3.40	2.35	2.14	.524	1.35	.330	.146	8.5	8.9

Matrix of means for *P. nelsoni* and *P. superior* (standardized at 40 mm height + width)

	COLOR5	LOWCOL	PRWIDT	PRHIGH	WIDTH2	HEIGH2	WIDTH3	HEIGH3	WIDTH4	HEIGH4	WIDTH5	HEIGH5	TSIZE5	RATIO5	DANGLE
P.n. nelsoni															
SH5 (Main)		.323	2.19	.318	3.39	1.21	4.85	2.28	6.76	4.03	9.46	6.79	16.25	1.39	56.1
SH5 (Bird)		.328	2.44	.318	3.75	1.22	5.19	2.47	6.87	4.60	9.17	7.72	16.89	1.19	57.3
SH5 (Coquina)	.092	.235	2.25	.281	3.38	1.01	4.81	1.98	6.58	3.71	8.94	6.23	15.18	1.43	56.0
SH89		.395	2.37	.356	3.59	1.40	5.07	2.51	7.13	4.54	10.07	7.56	17.78	1.31	57.7
SHP9		.336	2.20	.287	3.39	1.22	4.87	2.31	6.80	4.15	9.39	7.10	16.49	1.32	58.0
SHP2		.304	2.43	.211	3.78	0.863	5.46	1.95	7.71	3.76	11.17	6.41	17.59	1.74	58.2
SHP3	.359	.324	2.34	.272	3.53	0.967	5.03	1.94	6.96	3.57	9.75	6.25	16.00	1.60	54.0
SH30		.387	2.38	.283	3.63	1.24	5.19	2.37	7.28	4.32	10.13	7.31	17.44	1.39	56.9
SH65	.498	.355	2.40	.290	3.66	1.12	5.28	2.17	7.50	4.03	10.94	7.17	18.11	1.52	55.3
SH97		.294	2.05	.272	3.35	0.848	5.10	1.68	7.34	3.47	10.71	6.62	17.34	1.62	58.5
HP64		.444	2.28												
SG18	.400	.341	2.35	.238	3.71	0.997	5.36	2.08	7.68	3.85	11.00	6.83	17.83	1.61	55.3
SG68	.330	.330	2.41	.314	3.75	1.21	5.34	2.35	7.56	4.24	10.70	7.19	17.89	1.49	56.4
P.n. callosus															
HP95		.288	2.04	.365	3.17	1.16	4.61	2.10	6.67	3.68	9.61	6.40	16.01	1.50	55.0
HP30		.287	1.95	.342	2.92	1.04	4.21	1.92	6.01	3.59	8.38	6.20	14.58	1.35	56.8
HP45	.391	.214	1.83	.323	2.83	1.01	4.09	1.89	5.71	3.39	7.78	5.89	13.67	1.32	57.2
HP86		.224	1.85	.310	2.95	0.937	4.36	1.79	6.28	3.21	8.94	5.71	14.66	1.57	56.7
HPP8	.631	.290	2.00	.391	3.04	1.26	4.39	2.19	6.15	3.76	8.69	6.29	14.98	1.38	56.5
HP(?)[1]		.237	1.84	.312	2.75	1.06	3.97	1.93	4.87	3.41	7.47	5.94	13.41	1.26	58.0
HP84 and 88			2.04	.307	2.99	1.03	4.20	1.82	5.82	3.07	8.24	5.03	13.27	1.64	53.7
P.s. superior															
SH34	.277	.250	2.40	.305	3.50	1.21	4.76	2.48	6.12	4.61	7.37	7.41	14.76	0.994	59.6
SH5 (Bird)	.272	.277	2.13	.335	3.17	1.25	4.29	2.37	5.39	4.26	6.67	7.01	13.67	0.951	61.2
SH9[2]		.227	2.54	.372	3.65	1.56	4.84	3.12	6.18	5.58	7.44	9.37	16.81	0.794	54
P.s. arenicolus															
HP63		.206	1.95	.330	2.96	1.06	4.23	1.93	5.82	3.50	7.60	6.18	13.78	1.23	56.6
HP100		.221	1.97	.333	3.04	1.03	4.36	1.86	6.12	3.45	8.18	6.26	14.45	1.31	56.8
HP11		.221	2.05	.314	3.20	1.07	4.48	2.07	6.07	3.82	7.75	6.67	14.42	1.16	57.3
HP(?)[3]		.201	2.05	.348	3.07	1.21	4.29	2.28	5.67	4.15	7.17	7.10	14.27	1.01	55.8

[1] From Sayles collection labelled "S. Shore Harrington Sound."
[2] Either *P.s. superior* or *P.n. nelsoni.*
[3] From Bermuda Museum labelled "Bermuda."

MATRIX OF MEANS FOR *P. NELSONI* AND *P. SUPERIOR* (continued)

	KVALUE	INFORM	UMBILC	APLONG	ALDIVW	APHIGH	RELSPI	INNLIP	OUTCAR	LOWOFF	LOWECC	UPPOFF	UPPECC	Total height	CALLUS
P.n. nelsoni															
SH5 (Main)	1.86	260	2.26	11.75	1.21	9.69	.629	8.76	5.82	2.32	.197	4.02	.342	15.4	0.229
SH5 (Bird)	2.28	240	2.60	11.84	1.28	9.27	.606	8.18	6.07	5.21	.440	4.42	.373	15.3	0.033
SH5 (Coquina)	2.14	217	2.23	11.73	1.23	9.52	.610	8.39	5.86	4.87	.415	4.42	.377	15.6	0.056
SH89	1.89	270	2.54	12.11	1.26	9.63	.651	8.44	6.20	3.76	.310	4.26	.351	14.8	0.102
SHP9	1.87	275	2.38	12.44	1.32	9.45	.622	8.59	6.03	2.98	.239	4.34	.349	15.2	0.020
SHP2	2.07	173	3.05	13.29	1.43	9.31	.700	8.88	6.28	3.76	.283	5.03	.378	13.3	0.010
SHP3	2.01	197													0.593
SH30	1.80	262	2.81	12.17	1.27	9.58	.665	8.32	6.23	4.12	.339	4.23	.347	14.4	0.108
SH65	1.96	224	2.68	12.65	1.37	9.26	.652	8.82	5.95	2.68	.212	4.32	.341	14.2	0.072
SH97	2.16	171	2.84	12.71	1.35	9.39	.676	9.12	6.50	2.93	.230	4.67	.368	13.9	0.000
HP64															
SG18	1.88	221	2.98	12.62	1.42	8.88	.648	8.33	6.55	3.57	.283	4.84	.383	13.7	0.190
SG68	1.85	242	2.56	12.54	1.35	9.27	.648	8.32	6.13	3.72	.297	4.61	.368	14.3	0.079
P.n. callosus															
HP95	1.81	254	2.07	11.77	1.21	9.73	.653	8.53	5.76	2.83	.240	3.75	.319	14.9	0.977
HP30	1.97	240	2.04	11.59	1.16	9.97	.619	8.53	6.06	2.74	.236	3.88	.335	16.1	0.557
HP45	2.03	246	1.47	11.38	1.13	10.04	.608	8.62	6.00	3.82	.336	3.87	.340	16.5	0.688
HP86	1.92	215	2.08	12.08	1.25	9.63	.629	8.94	6.35	4.98	.413	4.33	.358	15.3	1.157
HPP8	1.77	290	1.89	11.19	1.19	9.40	.610	8.42	5.61	3.59	.320	3.60	.321	15.4	0.659
HP(?)[1]	2.00	270	1.35	11.26	1.17	9.66	.589	8.41	5.95	4.48	.398	3.72	.330	16.4	0.419
HP84 and 88	1.80	246	2.43	10.91	1.15	9.52	.591	8.48	5.88	3.48	.319	3.79	.348	16.1	1.940
P.s. superior															
SH34	2.82	258	1.41	11.01	1.09	10.10	.552	7.59	6.25	4.67	.424	4.23	.384	18.3	0.000
SH5 (Bird)	2.66	290	1.16	10.43	1.04	10.03	.528	7.37	6.34	5.59	.536	4.45	.427	19.0	0.033
SH9[2]	2.60	327													
P.s. arenicolus															
HP63	2.23	243	1.53	10.71	1.15	9.31	.538	8.11	5.77	5.09	.475	3.73	.349	17.3	0.082
HP100	2.18	227	1.96	11.12	1.10	10.13	.603	8.63	5.83	4.94	.444	3.57	.321	16.8	0.144
HP11	2.37	238	1.56	10.74	1.11	9.67	.559	8.14	5.79	4.48	.417	3.21	.299	17.3	0.098
HP(?)[3]	2.40	280	1.65	10.52	1.08	9.29	.510	7.62	5.91	5.65	.537	3.87	.368	18.2	0.016

[1] From Sayles collection labelled "S. Shore Harrington Sound."
[2] Either *P.s. superior* or *P.n. nelsoni.*
[3] From Bermuda Museum labelled "Bermuda."

MATRIX OF MEANS FOR *P. BERMUDENSIS* (STANDARDIZED AT 30 MM HEIGHT + WIDTH)

	ONSEUP	ONSELO	LOWCOL	COLOR3	COLOR4	COLOR5	PRDEGR	PRWIDT	PRHIGH	WIDTH1	HEIGH1	WIDTH2	HEIGH2	WIDTH3	HEIGH3	WIDTH4	HEIGH4	WIDTH5	HEIGH5
P.b. zonatus																			
SH5	5.12	3.58	.322		.708	.741	607.7	2.16	.289	2.12	.487	3.20	0.843	4.59	1.50	6.38	2.88	8.52	5.46
SHP5			.364				653.6	2.20	.309	2.09	.509	3.12	0.879	4.48	1.57	6.02	2.97	7.76	5.43
SHP6	5.47	4.59	2.95		.605	.682	612.1	2.14	.288	2.08	.487	3.07	0.843	4.37	1.48	5.97	2.71	7.80	5.05
SHP1	5.31	4.14	.306		.610	.650	598.3	2.19	.316	2.11	.494	3.20	0.814	4.58	1.46	6.30	2.84	8.46	5.20
H1	5.17	4.35	.393		.800	.822	651.9	2.14	.327	2.17	.588	3.25	1.08	4.68	1.96	6.49	3.65	8.58	6.72
H87	5.12	4.13	.336		.774	.779	712.1	2.24	.362	2.25	.639	3.36	1.18	4.80	2.08	6.57	3.73	8.62	6.68
H2	5.18	4.32	3.67		.769	.791	633.7	2.18	.344	2.21	.596	3.36	1.10	4.85	2.01	6.82	3.71	9.04	6.79
H49		5.08	.415		.503	.506	617.2	2.17	.336	2.21	.618	3.33	1.11	4.85	1.95	6.73	3.63	8.81	6.65
H51		4.32	.405		.478	.467	624.6	2.14	.345	2.20	.632	3.32	1.13	4.84	2.01	6.68	3.73	8.59	6.78
P6		3.23	.375	.482	.518	.568	660.2	2.17	.363	2.21	.661	3.35	1.24	4.90	2.16	6.80	4.00	8.80	7.15
P1			.370		.809	.836	583.7	2.14	.327	2.16	.610	3.31	1.16	4.88	2.07	6.87	4.00	9.28	7.14
P87			.368		.869	.877	620.7	2.17	.331	2.22	.625	3.36	1.16	4.88	2.11	6.75	3.95	8.78	7.13
P50		4.09	.356	.490	.476	.477	657.2	2.20	.347	2.22	.639	3.36	1.13	4.90	2.03	6.82	3.83	8.86	6.85
SG17			.383				595.2	2.09	.320	2.07	.567	3.15	1.02	4.52	1.80	6.35	3.31	8.49	6.07
SG37	5.00	4.04	.410		.786	.788	618.5	2.17	.324	2.11	.581	3.18	1.05	4.58	1.85	6.28	3.52	8.19	6.41
SG41	5.10	3.88	.374		.746	.779	619.0	2.14	.336	2.12	.581	3.19	1.09	4.56	1.87	6.41	3.39	8.55	6.12
SG31			.394		.753	.783	611.7	2.17	.285	2.18	.567	3.36	1.09	4.92	2.05	6.76	4.00	9.15	7.19
SG66			.309				597.1	1.99	.291	2.02	.538	3.08	0.981	4.49	1.83	6.21	3.45	8.16	6.31
S17			.390			.769	636.5	2.12	.372	2.17	.654	3.28	1.16	4.78	2.06	6.65	3.85	8.97	7.00
S36	4.80	4.05	.389		.820	.792	691.8	2.17	.319	2.27	.618	3.44	1.16	5.01	2.11	6.93	4.07	9.29	7.34
S75		4.29	.430		.696	.663	709.0	2.20	.344	2.25	.639	3.41	1.16	4.98	2.06	6.74	4.01	8.60	7.14
S73		4.39	.361		.524	.492	697.6	2.14	.403	2.17	.719	3.31	1.26	4.87	2.23	6.62	4.26	8.94	7.83
P.b. fasolti																			
SH53		5.41	.293				548.1	2.00	.247	1.98	.421	3.03	0.734	4.43	1.26	6.26	2.35	8.77	4.25
P.b. siegmundi																			
H10		4.53	.328		.441	.428	659.2	2.13	.385	2.19	.683	3.36	1.23	4.95	2.14	7.12	3.89	9.53	7.04
P.b. sieglindae																			
H44	5.38	4.50	.379		.752	.769	629.6	2.18	.338	2.20	.574	3.36	1.03	4.92	1.87	7.09	3.39	9.87	6.11
P44		4.82	.374			.658	621.1	2.17	.345	2.22	.581	3.40	1.03	5.03	1.90	7.30	3.49	9.95	6.59
P.b. bermudensis																			
SG16			.300				593.4	2.11	.350	2.09	.639	3.20	1.15	4.69	2.01	6.79	3.52	9.74	6.73
S27			.310				664.2	2.16	.424	2.23	.718	3.41	1.32	5.09	2.26	7.27	4.16	9.62	6.97
S21b			.313			.734	629.7	2.16	.343	2.18	.618	3.34	1.10	4.94	1.95	7.32	3.46	10.27	6.28
S21a			.289			.644	600.1	2.12	.362	2.17	.661	3.32	1.17	4.91	2.04	7.24	3.72	9.76	6.42
R80			.350				620.8	2.05	.351	2.01	.668	3.08	1.23	4.44	2.24	6.19	4.03	8.08	6.55
R79			.349				593.0	2.08	.381	2.09	.705	3.18	1.29	4.69	2.25	6.73	4.04	9.07	7.03
R78			.315				584.7	2.04	.409	2.04	.719	3.07	1.31	4.48	2.32	6.31	4.16	8.09	6.92
R82			.285				584.2	2.06	.360	2.07	.661	3.12	1.21	4.51	2.20	6.34	3.92	8.21	6.67
R81			.313				634.4	2.11	.401	2.14	.719	3.23	1.31	4.69	2.24	6.73	3.96	9.00	6.68
R83			.335				571.5	2.04	.389	2.05	.712	3.10	1.29	4.53	2.27	6.44	4.12	8.61	6.88
hybrids *P. cupula* × *P. bermudensis*																			
?69		2.86	.236	.275	.270	.261	635.3	2.20	.438	2.16	.821	3.26	1.50	4.71	2.72	6.04	5.09	7.66	8.64
H3			.261				552.5	2.04	.332					4.40	1.84	5.98	3.39	7.72	6.10

MATRIX OF MEANS FOR *P. BERMUDENSIS* (continued)

	TSIZE5	RATIO5	PSANGL	DANGLE	KVALUE	INFORM	UMBILC	APLONG	ALDIVW	APHIGH	RELSPI	INNLIP	OUTCAR	LOWOFF	LOWECC	UPPOFF	UPPECC	Total height	CALLUS
P.b. zonatus																			
SH5	13.98	1.56	43.8	56.0	2.32	.173	2.38	8.79	1.19	7.37	.676	6.63	4.12	2.79	.317	2.86	.326	10.9	.223
SHP5	13.19	1.42	51.5	59.6	2.42	.184	2.22	8.86	1.21	7.34	.667	6.68	4.08	3.26	.368	2.76	.311	11.0	.180
SHP6	12.85	1.55	44.8	59.7	2.29	.186	2.40	8.54	1.17	7.29	.657	6.53	4.06	3.24	.380	2.73	.320	11.1	.141
SHP1	13.66	1.63	43.6	58.4	2.37	.158	2.26	8.97	1.23	7.27	.667	6.88	4.06	3.24	.361	2.90	.323	10.9	.151
H1	15.30	1.28	50.5	58.5	2.22	.241	2.01	8.80	1.26	6.96	.621	6.44	4.33	4.01	.456	3.09	.351	11.2	.259
H87	15.30	1.29	50.1	58.4	2.18	.244	1.92	8.75	1.30	6.75	.619	6.39	4.25	4.08	.466	3.02	.346	10.9	.269
H2	15.83	1.33	45.9	54.7	2.16	.227	1.74	8.84	1.35	6.55	.618	6.36	4.02	2.70	.452	2.83	.337	10.6	.341
H49	15.46	1.32	50.3	56.5	2.14	.238	1.96	8.87	1.37	6.48	.623	6.31	4.23	3.93	.443	3.27	.369	10.4	.259
H51	15.37	1.27	51.4	58.0	2.21	.231	2.07	8.71	1.32	6.59	.605	6.12	4.48	4.05	.465	3.32	.381	10.9	.265
P6	15.95	1.23	51.5	58.6	2.13	.260	1.89	8.70	1.33	6.57	.597	6.23	4.32	3.83	.440	3.01	.346	11.0	.200
P1	16.42	1.29	45.8	59.1	2.08	.250	1.69	9.02	1.31	6.91	.634	6.35	4.57	4.16	.461	3.36	.373	10.9	.295
P87	15.92	1.23	47.8	59.4	2.18	.244	1.74	8.72	1.28	6.81	.619	6.31	4.48	4.60	.528	3.15	.361	11.0	.239
P50	15.71	1.29	49.8	56.3	2.18	.234	1.91	8.81	1.30	6.76	.620	6.20	4.50	4.26	.483	3.28	.372	10.9	.193
SG17	14.56	1.40	46.4	57.8	2.13	.224	2.22	8.63	1.28	6.76	.644	6.30	4.00	3.76	.435	2.81	.326	10.5	.164
SG37	14.61	1.28	50.0	58.2	2.28	.229	2.00	8.47	1.29	6.55	.570	6.47	4.01	3.81	.449	2.69	.317	11.5	.229
SG41	14.67	1.40	44.2	54.3	2.08	.236	1.77	8.95	1.37	6.55	.618	6.57	3.91	3.81	.425	2.75	.307	10.6	.111
SG31	16.36	1.27	47.9	55.8	2.21	.241	1.70	8.56	1.29	6.63	.603	6.37	4.26	4.06	.475	3.09	.362	11.0	.177
SG66	14.47	1.29	51.6	57.0	2.24	.225	2.03	8.81	1.28	6.87	.608	6.19	4.25	3.74	.425	3.16	.359	11.3	.010
S17	15.98	1.28	50.8	57.0	2.12	.245	1.99	8.83	1.28	6.92	.635	6.32	4.29	4.03	.456	3.07	.347	10.9	.275
S36	16.63	1.27	47.5	57.2	2.22	.236	1.80	9.02	1.35	6.70	.644	6.49	4.23	4.01	.449	2.99	.331	10.4	.236
S75	15.74	1.20	52.3	57.9	2.30	.242	2.03	8.74	1.20	7.26	.660	6.68	4.30	4.26	.487	2.83	.324	11.0	.465
S73	16.77	1.14	53.0	59.5	2.21	.262	1.92	8.59	1.19	7.21	.655	6.39	4.30	4.37	.508	2.79	.325	11.0	.551
P b. fasolti																			
SH53	13.02	2.06	32.2	53.0	2.02	.160	3.01	9.35	1.25	7.48	.748	6.63	4.05	1.70	.182	3.09	.330	10.0	.000
P.b. siegmundi																			
H10	16.57	1.35	45.1	54.3	1.99	.250	2.34	9.32	1.42	6.55	.662	6.05	4.35	3.04	.326	3.49	.374	9.9	.098
P.b. sieglindae																			
H44	15.98	1.61	36.7	55.0	1.95	.207	2.03	9.35	1.41	6.65	.693	6.64	4.14	2.39	.256	3.15	.336	9.6	.102
P44	16.54	1.51	39.4	54.7	2.03	.210	1.82	9.18	1.41	6.49	.656	6.48	4.24	2.53	.276	3.07	.334	9.9	.079
P.b. bermudensis																			
SG16	16.47	1.45	38.8	53.8	1.82	.250	2.43	9.37	1.35	6.95	.695	6.57	4.40	3.16	.337	3.49	.372	10.0	.000
S27	16.59	1.38	41.7	53.9	1.91	.262	2.11	9.48	1.39	6.81	.668	6.63	4.40	4.23	.446	3.44	.363	10.2	.000
S21b	16.54	1.64	34.4	53.3	1.82	.226	2.51	9.45	1.41	6.70	.720	6.53	4.24	2.47	.261	3.34	.354	9.3	.000
S21a	16.18	1.52	38.6	55.1	1.85	.244	2.47	9.52	1.41	6.77	.691	6.73	4.45	3.98	.418	3.41	.358	9.8	.000
R80	14.62	1.23	43.2	54.3	2.03	.284	2.09	8.92	1.28	6.95	.644	6.52	4.45	3.57	.401	3.39	.380	10.8	.000
R79	16.10	1.29	45.2	56.4	1.91	.283	2.23	8.67	1.20	7.24	.652	6.49	4.03	2.86	.329	3.64	.420	11.1	.000
R78	15.02	1.17	46.7	54.9	2.01	.293	2.26	8.45	1.29	6.55	.570	6.41	3.62	3.56	.421	2.64	.313	11.5	.000
R82	14.88	1.23	45.5	56.0	2.03	.273	2.22	8.83	1.22	7.26	.648	6.57	4.16	3.41	.386	3.17	.359	11.2	.000
R81	15.69	1.35	40.7	55.3	1.86	.285	2.45	8.80	1.21	7.28	.668	6.41	4.03	2.76	.314	2.97	.338	10.9	.000
R83	15.49	1.25	41.8	56.2	1.96	.289	2.14	8.72	1.26	6.91	.628	6.45	4.15	3.36	.386	3.03	.348	11.0	.000
hybrids *P. cupula* × *P. bermudensis*																			
269	16.30	0.89	60.8	61.8	2.44	.326	1.60	7.56	1.11	6.81	.536	5.82	4.11	4.45	.588	2.81	.372	12.7	.252
H3	13.82	1.27	53.9	55.7	2.35	.319	1.63	8.72	1.27	6.86	.602	6.56	4.20	4.00	.459	2.98	.342	11.4	.000

Plate 1. *Poecilozonites cupula* and coloration of *P. bermudensis*

Figures

1. *Poecilozonites cupula cupula* Gulick. From locality 63, Pembroke Formation. Coloration $12^{n}3$. MCZ 29006. × 2½.

2. *Poecilozonites cupula dalli* (Gulick). From locality 4, Harrington Formation. Coloration $02^{n}3$. MCZ 29007. × 2½.

3. *Poecilozonites cupula cupuloides* (Peile). From locality 9, Walsingham Formation. Coloration $1^{f}00$. MCZ 29008. × 2½.

4. *Poecilozonites cupula multispira* new subsp. Holotype from locality 84, Harrington Formation. Coloration 023. MCZ 29009. × 2½.

5. *Poecilozonites cupula triangularis* new subsp. Holotype from locality 46, Harrington Formation. Coloration 023. MCZ 29010. × 2½.

6. *Poecilozonites bermudensis zonatus* Verrill. From locality 6, Pembroke Formation. Illustrated to show coloration of this subspecies in western Bermuda—023. MCZ 28995. × 2.

7. *Poecilozonites bermudensis zonatus* Verrill. From locality 41, Southampton Formation. Illustrated to show coloration of this subspecies in eastern Bermuda—123. MCZ 28994. × 2.

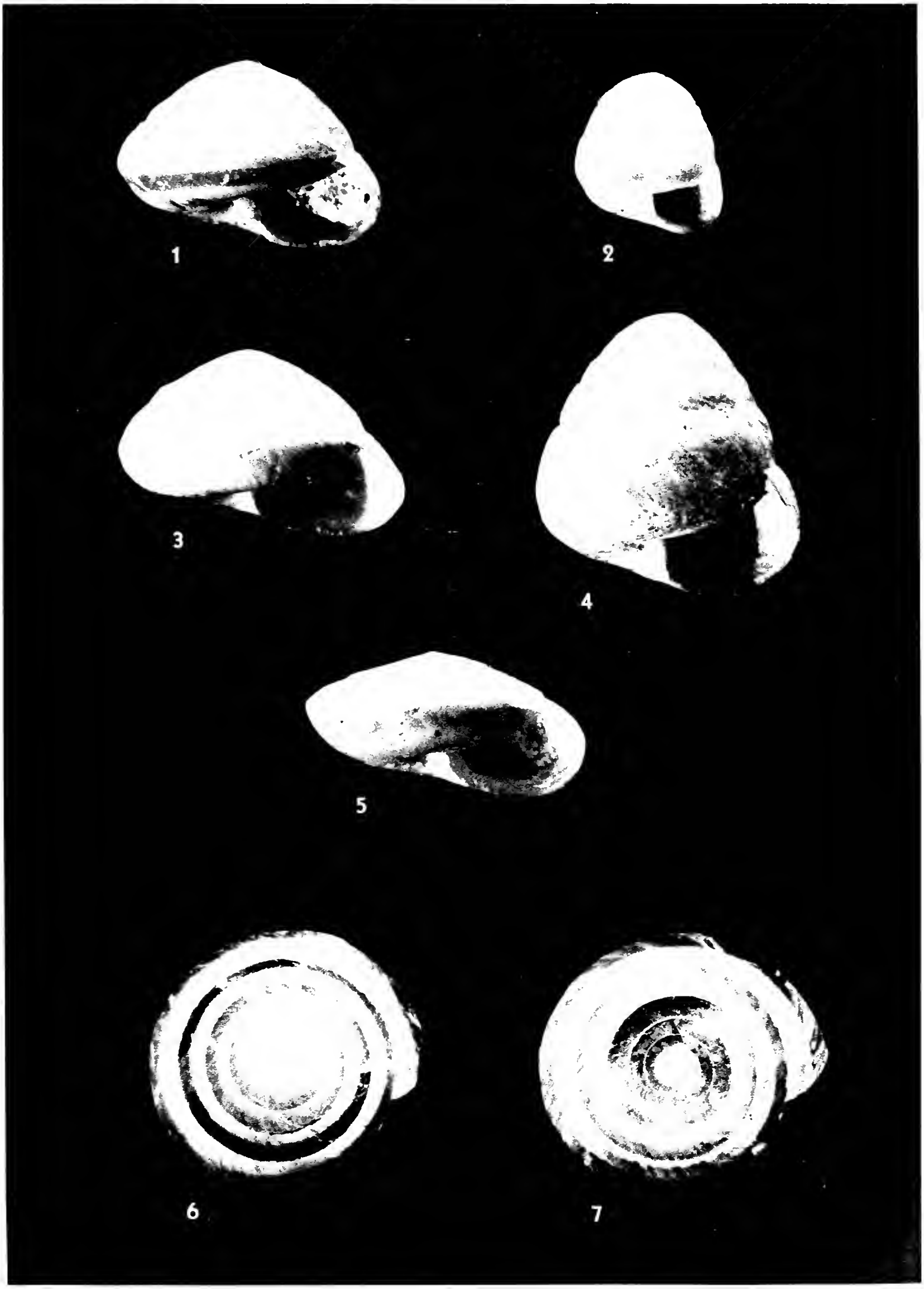

PLATE 1

Plate 2. *Poecilozonites nelsoni* and *P. superior*

Figures 1–5 are arranged to show increasing height of spire among local populations of *P.n. nelsoni.*

Figures

1. *Poecilozonites nelsoni nelsoni* (Bland). Holotype of *P. nelsoni discoides* Gulick. From locality P2, Shore Hills Formation. ANSP 58084. × 1.

2. *Poecilozonites nelsoni nelsoni* (Bland). From locality 18, St. George's Formation. MCZ 29011. × 1.

3. *Poecilozonites nelsoni nelsoni* (Bland). From locality 30, Shore Hills Formation. MCZ 29012. × 1.

4. *Poecilozonites nelsoni nelsoni* (Bland). Topotype of *P. nelsoni conoides* Verrill. From locality P2, Shore Hills Formation. MCZ 29013. × 1.

5. *Poecilozonites nelsoni nelsoni* (Bland) or *P. superior superior* new sp. From locality 9, Shore Hills Formation. MCZ 29014. × 1.

6. *Poecilozonites nelsoni nelsoni* (Bland). Would-be holotype of Pilsbry's manuscript name *P. nelsoni gulickiana.* From locality P3, Shore Hills Formation. ANSP 131582. × 1.

7. *Poecilozonites nelsoni nelsoni* (Bland). From locality 5 (Bird Fissure), Shore Hills Formation. MCZ 29015. × 1.

8. *Poecilozonites superior superior* new sp. Holotype from locality 5 (Bird Fissure), Shore Hills Formation. MCZ 29016. × 1.

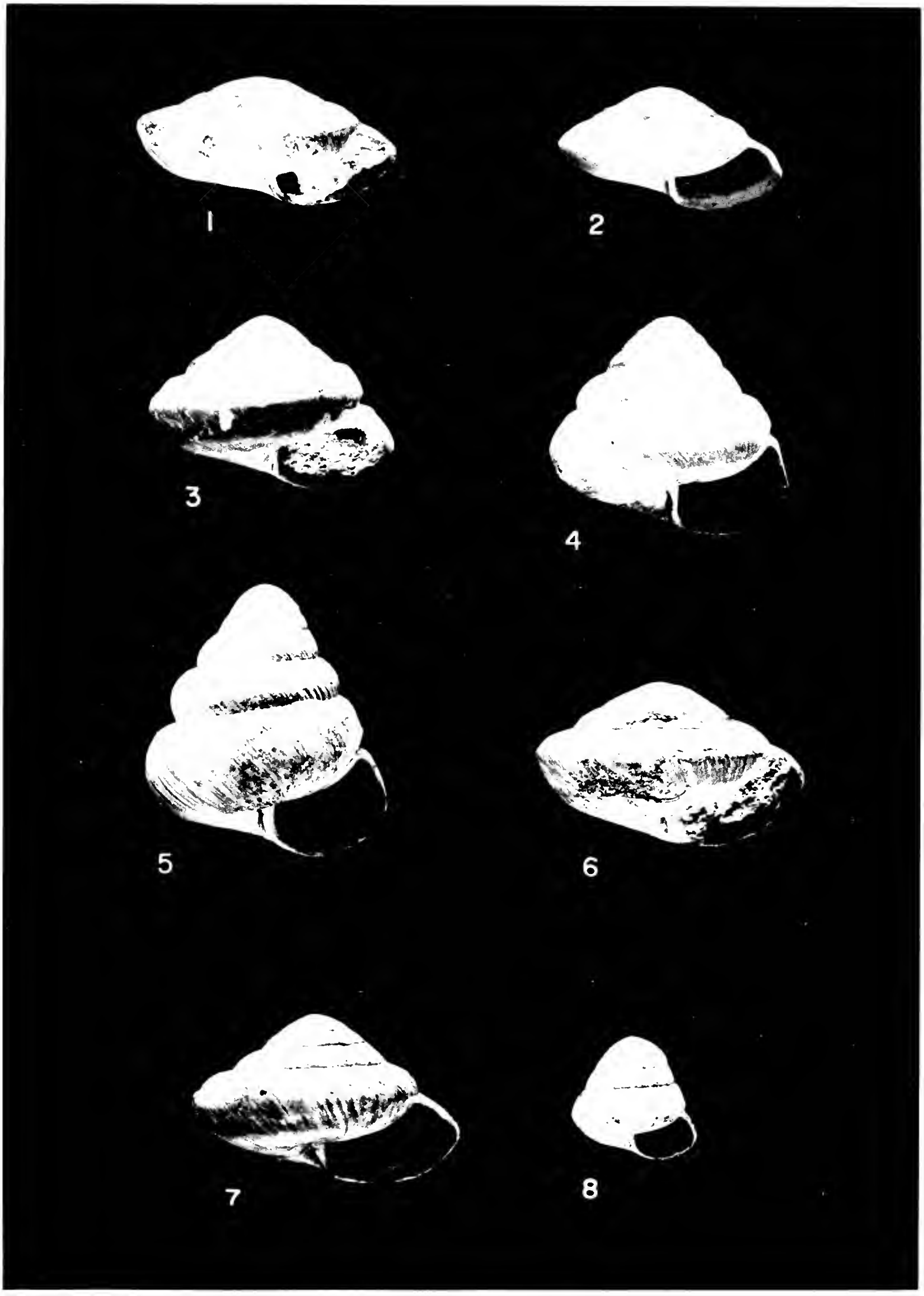

PLATE 2

Plate 3. *Poecilozonites nelsoni, P. superior,* and protoconch of *P. bermudensis*

Figures

1. *Poecilozonites nelsoni callosus* Gulick. From locality 45, Harrington Formation. Note 023 coloration. MCZ 29017. × 1.

2. *Poecilozonites nelsoni callosus* Gulick. Holotype from locality P8, Harrington-Pembroke Formations. ANSP 58086. × 1.

3. *Poecilozonites nelsoni callosus.* From locality 84, Harrington-Pembroke Formations. MCZ 29018. × 1.

4. *Poecilozonites superior arenicolus* new subsp. Holotype from locality 11, Pembroke Formation. MCZ 29019. × 1.

5. *Poecilozonites superior arenicolus* new subsp. From Bermuda Museum, locality unknown. Note 103 coloration. MCZ 29020. × 1.

6. *Poecilozonites bermudensis bermudensis* (Pfeiffer). From locality 78. Recent. $\frac{1}{2}$ whorled specimen to show form of juvenile. MCZ 29000. × 18.

7. *Poecilozonites bermudensis bermudensis* (Pfeiffer). From locality 78. Recent. Note transition from protoconch to post-embryonic shell $\frac{1}{2}$ whorl before terminus. MCZ 29000. × 18.

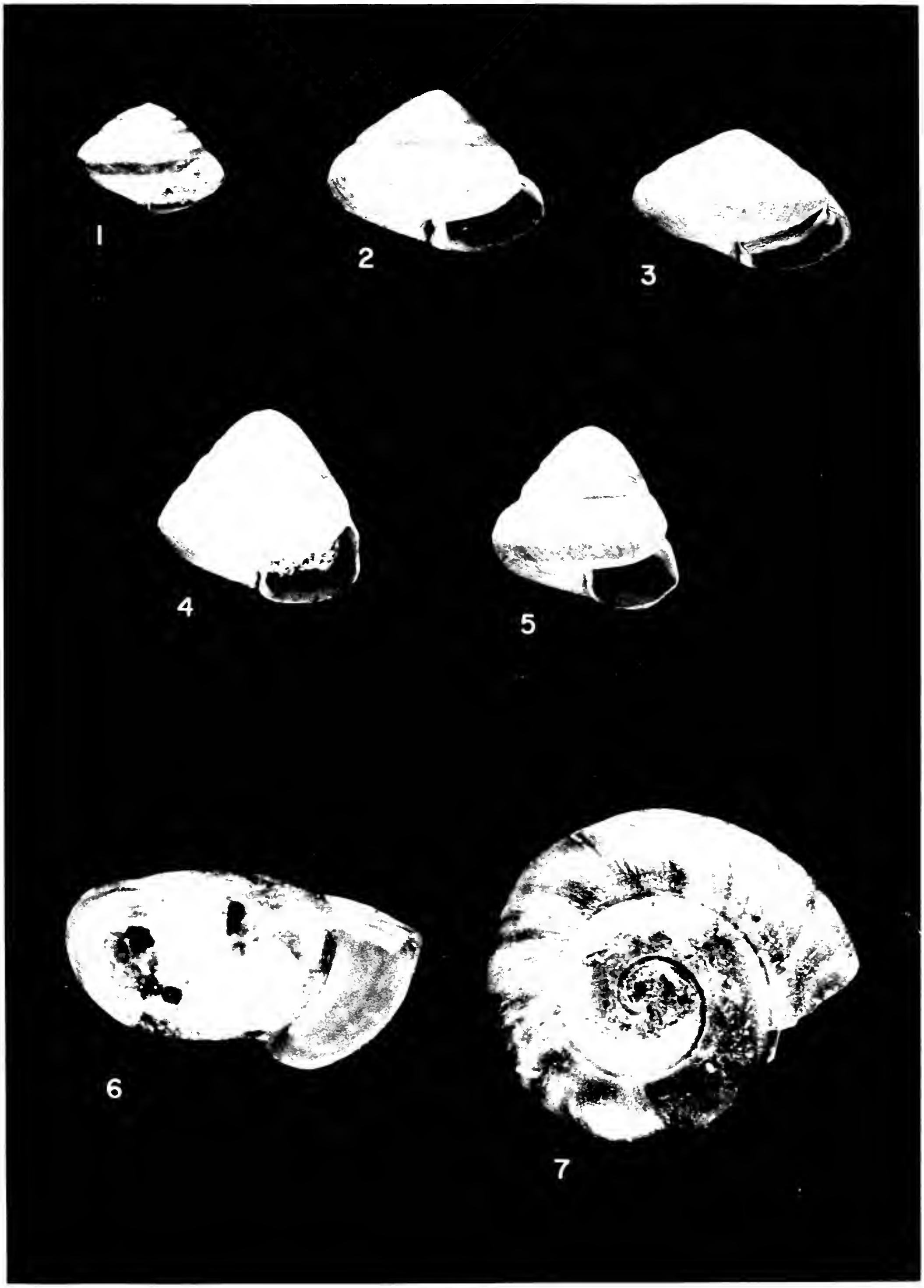

PLATE 3

Plate 4. *Poecilozonites bermudensis*

Figures 1–6 depict ancestral and paedomorphic subspecies of this taxon. Figure 1 enlarged × 2; others enlarged to same width. Actual widths of specimens: 1 = 19.7 mm, 2 = 11.5 mm, 3 = 22.2 mm, 4 = 21.5 mm, 5 = 20.2 mm, 6 = 23.0 mm.

Figures

1. *Poecilozonites bermudensis zonatus* Verrill. From locality 73, Southampton Formation. MCZ 28987.

2. *Poecilozonites bermudensis zonatus* Verrill. From locality 73, Southampton Formation. Juvenile specimen (3 6/8 whorls) enlarged to show similarity of shape with adult paedomorphs. MCZ 28988.

3. *Poecilozonites bermudensis fasolti* new subsp. Holotype from locality 53, Shore Hills Formation. MCZ 28989.

4. *Poecilozonites bermudensis siegmundi* new subsp. Holotype from locality 10, Harrington Formation. MCZ 28990.

5. *Poecilozonites bermudensis sieglindae* new subsp. Holotype from locality 44, Harrington Formation. MCZ 28991.

6. *Poecilozonites bermudensis bermudensis* (Pfeiffer). From locality 21, Southampton Formation. MCZ 28992.

7. *Poecilozonites bermudensis bermudensis* (Pfeiffer). From locality 78, Recent. Illustrated to show persistence of juvenile color flammulation in paedomorphs. MCZ 28993. × 2.

8. *Poecilozonites bermudensis zonatus* Verrill. From locality 41, Southampton Formation. Typical coloration of non-paedomorphs. MCZ 28994. × 2.

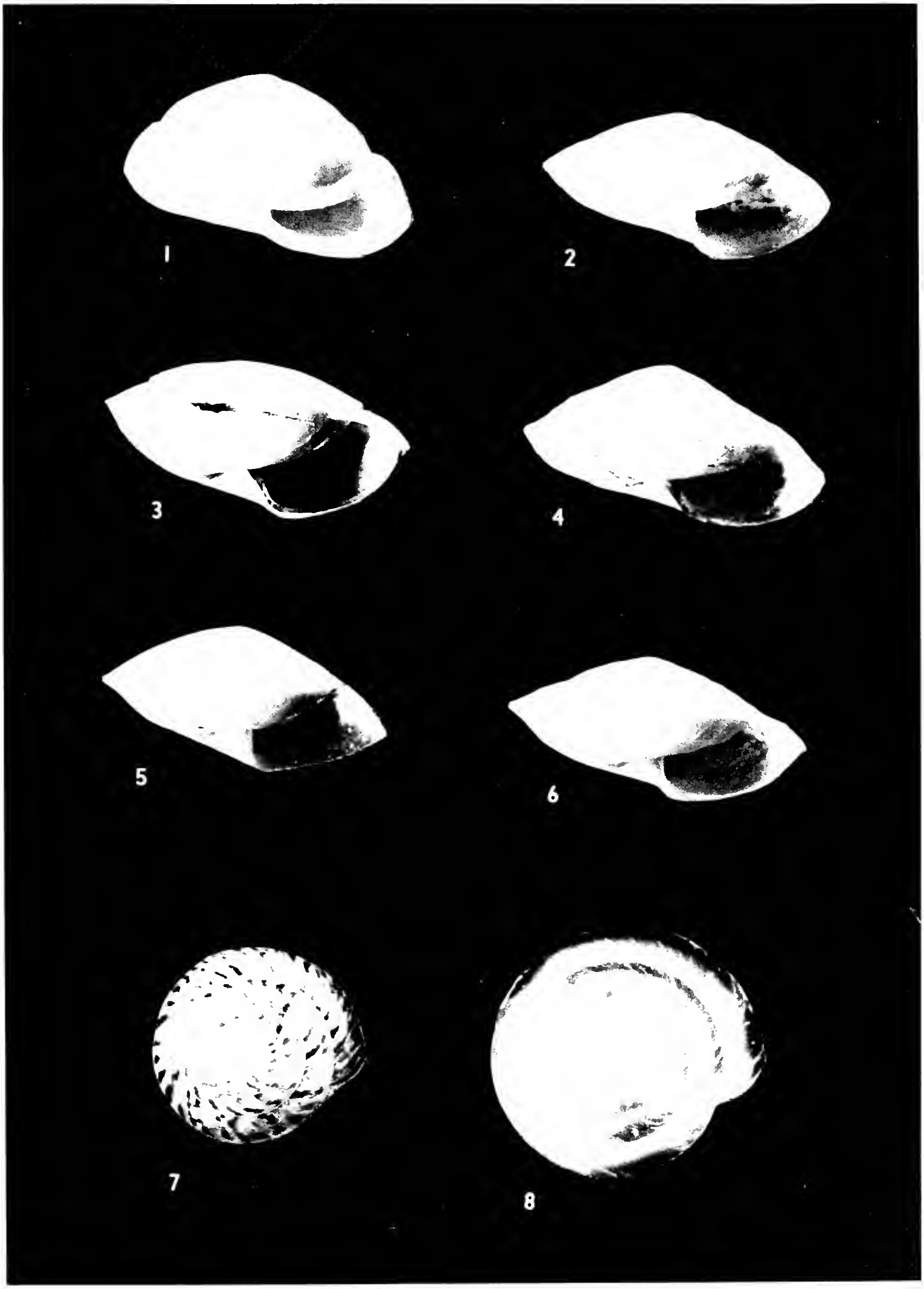

PLATE 4

Plate 5. Hybrids *Poecilozonites cupula* × *P. bermudensis* and coloration of *P. bermudensis*

Figures

1. Hybrids, *Poecilozonites cupula* × *P. bermudensis*. From locality 3, Harrington Formation. 1a, *cupula*-like coloration $12^{n}3$. 1b, intermediate. 1c, *bermudensis*-like coloration 1(23). MCZ 29004. × 2.

2. Hybrids, *Poecilozonites cupula* × *P. bermudensis*. From locality 69, formation unknown. Intermediate in color and form. MCZ 29005. × 2.

3. *Poecilozonites bermudensis zonatus* Verrill. From locality 67, formation unknown. 12(3S) coloration. MCZ 29001. × 2.

4. *Poecilozonites bermudensis zonatus* Verrill. From locality 5, Shore Hills Formation. 123 coloration. MCZ 29002. × 2.

5. *Poecilozonites bermudensis zonatus* Verrill. From locality 36, Southampton Formation. Illustrated to show "faded" color variation in which bands of color are replaced by lines at the previous band peripheries. MCZ 29003. × 2.

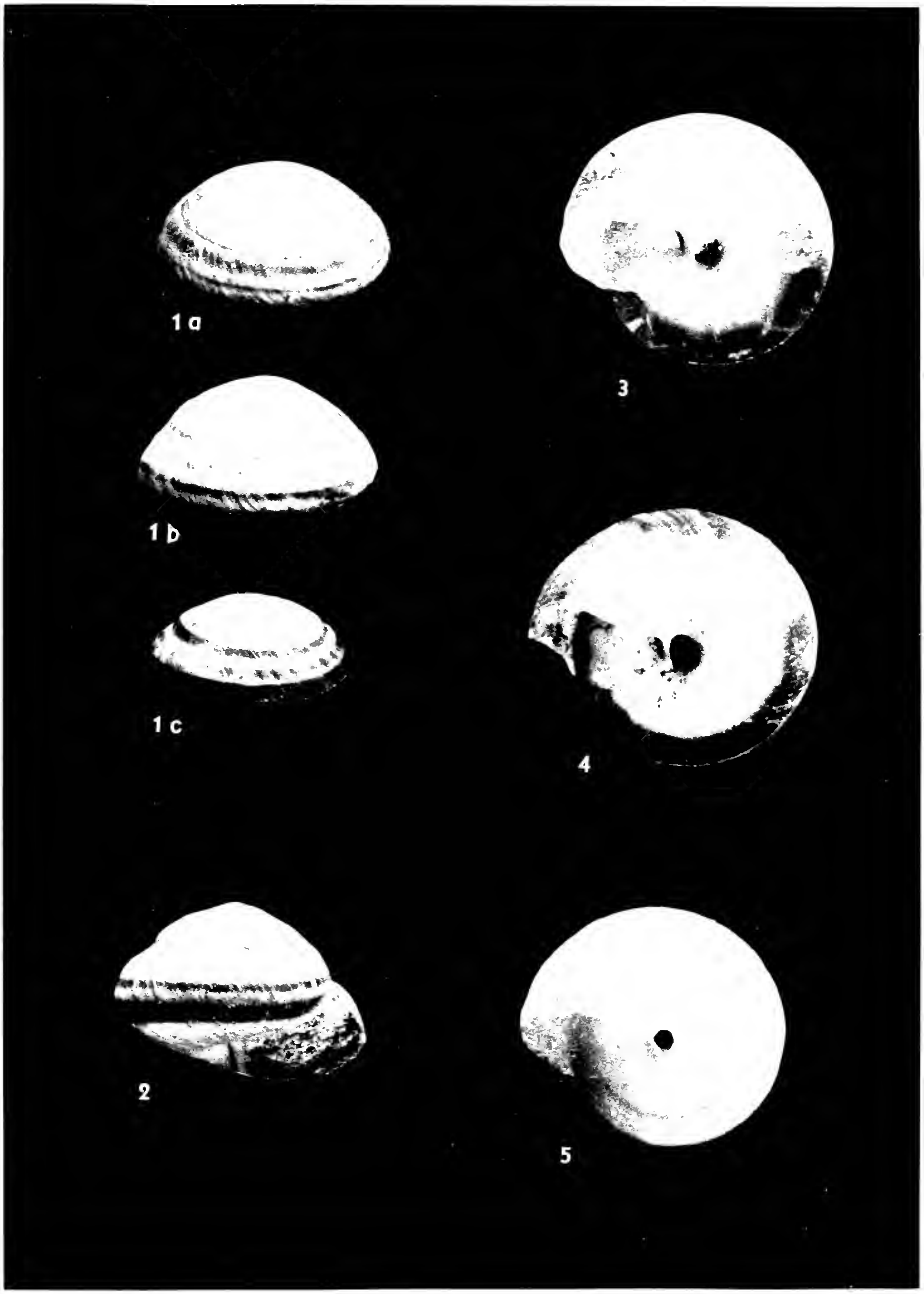

PLATE 5

Date Due

~~APR 30 1985~~	